PARASITOLOGY

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EDITED BY

GEORGE H. F. NUTTALL, F.R.S.

QUICK PROFESSOR OF BIOLOGY IN THE UNIVERSITY OF CAMBRIDGE

ASSISTED BY

EDWARD HINDLE, Ph.D.

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VOLUME X JANUARY, 1918 No. 2

ON THE DEVELOPMENT OF *ASCARIS LUMBRICOIDES* AND *A. MYSTAX* IN THE MOUSE.

PART II.

BY F. H. STEWART, M.A., D.Sc., M.B., MAJOR I.M.S.

(With Plate IV.)

IN previous papers[1] the migration of *Ascaris lumbricoides* in the rat and mouse has been traced to the point at which the larvae of the worm reach the trachea of these animals on the 8th day after infection. As the result of further experiments it is now possible to trace the migration through a further stage, namely that occurring from the 9th to the 15th days after infection. My experiments have not as yet been carried beyond the 15th day and in the following summary the statement that larvae occur in a given situation up to the 15th day is not intended to imply that they do not persist therein after that date.

Larvae are found in the mouths of infected mice on the 8th day, on which day they are also, as previously stated, abundant in the lungs and trachea. They persist in the lungs up to the 15th day. On the 9th day they begin to travel down the alimentary canal and may be found in small numbers in the stomach, small intestine and caecum. On the 10th day this stage is fully established, the larvae travel with some rapidity through the stomach and small intestine and accumulate in the caecum and upper colon where as many as 60–70 may occur. On this day they also commence to pass out in the faeces. The passage from the lungs to the caecum continues up to the 15th day and larvae occur in the faeces on the 16th day.

Between the 9th and 15th days the larvae increase in length. They measure from 1·3–2 mm. on the 10th day and 1·75–2·37 mm. on the 15th.

[1] *Brit. Med. Journ.* (July 1st and Oct. 7th, 1916); *Parasitology* (Feb. 26th, 1917), IX. 213–227, Pl. I. and 9 text-figs. The subject dealt with in the present paper has already been partly described in the *Brit. Med. Journ.* Dec. 2nd, 1916.

The above facts were ascertained from the following experiments:

(1) Experiments on Mice (k), (l), (m), (p) and (r) recorded in the *British Medical Journal*, December 2nd, 1916. In these experiments *Ascaris* larvae were found in the large intestine in four out of the five mice used, on the 9th, 10th, 11th and 12th days after infection. Larvae were also found in the faeces in two cases, on the 10th and 12th days.

(2) The following additional experiments are now recorded for the first time:

Mice (q), (s), (u) received doses of eggs 23 to 32 days old and were killed between the 10th and 13th days thereafter. No larvae were found in the lungs, intestine or faeces.

Mouse (v) received a dose from the same culture as (u) on September 4th. Not appearing ill, it received a second dose on October 21st and a third dose of another culture on November 13th. On the 16th day after the third infection one *Ascaris* larva was found in the faeces. The mouse was killed on the 18th day, but no larvae were found in the trachea or large intestine.

Mice (w) and (x) were killed as controls without infection. No nematodes were found in the lungs or trachea. Oxyurids were found in the colon. No forms resembling *Ascaris* larvae in any part of the intestine.

Mice (y) and (z) received doses of eggs of *A. suilla* aged 140 days and 41 days on October 13th. On the 10th day no larvae were found in the faeces. On the 11th day 5 larvae in the faeces, of which 2 moved languidly in salt solution. On the 12th, 13th, (and as regards mouse z) 14th and 15th days larvae were found in the faeces. Mouse (y) was killed on the 13th day. No larvae found in the lungs, 10 in the trachea, none in the mouth, stomach, or small intestine, 7 in the caecum, none in the colon. Mouse (z), killed on the 15th day, contained 2 larvae in the lungs, 10 in the caecum.

Thirteen mice (*Aa* to *Am*) died of cold or excessive infection; but 1 was examined. Larvae were found in the faeces of *Ai* on the 12th day.

Mouse *An* received a dose of eggs 31 days old on November 18th. Larvae were found in the faeces on the 9th, 10th, 11th and 12th days thereafter, not on the 14th and 16th days. The mouse was killed on the 17th day. No *Ascaris* larvae were found in the trachea or large intestine.

Mice *Ao*, *Ap* received doses of eggs 35 days old. Larvae were found in their faeces on the 9th and 12th days; they were killed on the 13th day. In *Ao* no larvae were found in the large intestine. In *Ap* three larvae were found in the caecum.

Mice *Aq*, *Ar* received doses of eggs 37 days old. *Ar* died on the 1st day. *Aq* was killed on the 11th day. Larvae were found in the lungs, none in the large intestine.

Mice *As*, *At* received doses of eggs 39 days old. They were killed on the 11th day. Nine larvae were found in the caecum of *As*. No examination was made of *At*, its entire large intestine being given to Pig 10.

Mice *Au*, *Av* received doses of eggs 52 days old. They were killed on the 10th day. Six larvae were found in the tip of the caecum of *Au*. The intestine of *Av* was given unopened to Pig 10.

The anatomy of larval Ascaris lumbricoides *L.* (A. suilla *Duj.*) *from the large intestine and faeces of the mouse between the* 10*th and* 15*th days after infection.*

The general shape (Pl. IV, fig. 1) is cylindrical, tapering slightly to the truncated head, sharply to the pointed tail. The head (Fig. 3) bears the three mamilliform lips characteristic of the genus. The shape of the tail is well shown in Fig. 11. The tip is curved toward the dorsum. The resemblance of this outline to the figures given by Leuckart of the tails of a young *Ascaris lumbricoides* (85 mm.) from man (*Menschl. Parasiten*, II. pt. 1, p. 217) and of young *A. mystax* from the dog (*ibid.*, pt. 2, p. 283) is worthy of note.

The cuticle is not ringed. In sections a fine sharply-marked and densely-staining outer membrane can be distinguished (Pl. IV, figs. 6, 7, 8) which is not present in the larvae found in the trachea or mouth (Figs. 9, 10) and is doubtless formed by reaction to the gastric and intestinal juices. Lateral membranes are present extending from the head to behind the anus (Figs. 6, 7, 8, 9, 10). These structures are first formed when the larvae are passing through the bronchi and trachea and have attained to a length of one millimetre. In a specimen measuring 1·5 mm. from the mouth, the membrane extends from the nerve-ring to the anus. The process of development of the membrane can be made clear by comparison of sections of larvae from the trachea and caecum. In the former the cuticle is raised along the lateral lines enclosing a space, triangular in cross section, the base of which is formed by the lateral lines. The cuticle forming each side of this triangle contains a slightly thickened and strongly staining lamina. The unspecialised and feebly staining cuticle of the body surfaces passes over the outer surface of these laminae. In the larvae from the caecum and faeces the laminae have become more thick and rigid and have partially coalesced, producing a sharp keel-like ridge with a flat base. The lateral membranes are curved toward the dorsum. Lateral membranes do not of course occur in the adult. They are doubtless formed to assist in the active swimming movements of the larvae.

Longitudinal lines. The lateral lines contain as a rule three nuclei in a cross section, dorsal and ventral lines one or two.

Muscle-fields. If the sections are counterstained with eosine the muscle cells can be seen to have assumed the folded form characteristic of the majority of adult nematodes.

The oesophagus (Pl. IV, figs. 2, 3) is club-shaped, anterior extremity slightly thickened, posterior extremity markedly so. The latter pro-

jects into the anterior end of the intestine. The external surface of the oesophagus is, as in the adult, covered with a sharply staining cuticle, a structure which is acquired in the passage along the alimentary canal of the rodent since it is not present in specimens from the trachea or mouth. In correspondence with the formation of this cuticular coat is the reduction of the cellular investment of the oesophagus, which is at its greatest development on the 5th or 6th day after infection. The body of the oesophagus is distinctly muscular.

The intestine is patent and is composed of a tesselated cylinder of hexagonal cells (Pl. IV, fig. 5). The anal canal is curved, expanded at the anterior extremity, and lined with cuticle.

The nerve ring is large and obvious (Figs. 2, 9) and possesses a cellular sheath. It lies immediately in front of the excretory aperture. An anal ganglion is formed by the ingrowth of the dorsal and lateral lines (Fig. 8).

The body of the unicellular excretory gland lies mainly between the left lateral line and the oesophagus (Figs. 2, 3, 4, 6, 10); a process however extends across the body and comes into contact with the right lateral line (Fig. 10). Its anterior extremity also passes toward the ventral line and meets the group of cells which contain the anterior portion of its duct. A considerable portion of the cell is occupied by the nucleus which is furnished with six chromatin masses of varying size. The excretory pore is situated in the ventral line immediately behind the nerve ring. From it the excretory duct (Figs. 2, 3, 4) passes backward through the group of cells of the ventral line referred to above (Figs. 2, 4), inclines to the left and enters the body of the gland in the left lateral line. It does not send a branch toward the right lateral line.

In younger larvae of 1 mm. or less in length the excretory gland appears to be confined to the left side of the body and not to send a process to the right lateral line. It is however also in contact with the ventral line and it appears probable that it originates from the ventral line and is homologous with the ventral gland of free-living nematodes. It is interesting to observe the manner in which the left-sided gland of the larva under consideration fits into the scheme of evolution of the excretory organ of nematodes as worked out by Jaegerskioeld (Jaegerskioeld, 'Beitr. zur Kennt. der Nematoden,' *Zool. Jahrb. Anat. Ontog.* VII. 449; Stewart, *Quart. Journ. Micr. Sci.*, L. 141). The unilateral organ of the younger larvae corresponds with that of *Ascaris decipiens*, the unequally bilateral organ of the older larvae with that of *A. rotundata*.

The rudiment of the gonads is situated about the junction of the

middle and posterior thirds of the body between the intestine and the ventral line (Fig. 5). It consists of a clearly defined lens-shaped group of cells.

The early life history of Ascaris mystax *Zeder* (A. marginata *Rud.*).

The development of the eggs of the *Ascaris* of the cat and dog has been studied by Nelson, Verloren, Davaine, Baillet and Grassi (Railliet, *Traité de Zoologie Méd. et Agric.*) and by Leuckart (*Menschl. Parasiten*, II. pt. 2, p. 275). I regret that at present I have not access to the works of these authors with the exception of the last-named.

Segmentation and the formation of an active embryo have been found to take place in water and damp earth. Davaine (quoted by Leuckart) states that development takes place also in a dry condition. Leuckart gives the period necessary for the formation of an active embryo in summer as four to ten weeks and in winter several months. The fully formed embryo differs from that of *A. lumbricoides* in being larger, 0·36–0·42 mm. in length as compared with 0·3–0·38 mm. in the latter, and in bearing a more distinct boring tooth on the ventral aspect of the mouth. There are no signs of the oesophageal bulb of the adult with the exception of a slight swelling of the posterior end of the oesophagus. He gives a figure of the embryo.

This investigator did not succeed by any means in bringing about the hatching of the eggs, nor did he produce any further development by feeding experiments. At one time he considered that he had empirically caused direct infection since he found young worms 3–4 mm. in length in the intestines of dogs which had been kept a long time in a kennel on the floor of which he found embryo-containing eggs. Repeated attempts at artificial infection in more than two dozen cats and dogs gave however negative results. He then attempted to find an intermediate host. He administered eggs of the worms to rabbits and mice and examined these animals after several weeks hoping to find encapsuled nematodes. No such nematodes were found. He states that the eggs passed unaltered through the alimentary canal of the mice.

In a later experiment he placed a number of young cats in a particular dwelling in which a number of animals had recently been kept. The latter had been found to harbour numerous young Ascarids. The cats were fed on bread only. After six to eight days the cats were killed. They proved to be infected with Ascarids 4–8 mm. long. In the stomach of one of them, a kitten eight weeks old, forty to sixty nematode larvae

were found which measured 0·4–0·6 mm. The stomach also contained fragments of straw and potato. No explanation could be given of the mode of entry of these larvae. No animal remains were found in the stomach or intestine to point to an intermediate host.

Grassi (I quote from Railliet's text-book) reared young puppies in a kennel soiled with egg-containing excrement. Their faeces contained *Ascaris* eggs on the 28th day and numerous Ascarids were found on section. A control experiment in sanitary surroundings proved negative. Grassi concluded that infection was direct.

Segmentation of the egg and development of the embryo.

I made cultures of the eggs of *A. mystax* in a damp atmosphere at a temperature between 25° and 30° C. Under these conditions development proceeded as follows: 1st day, unsegmented to three-cell stage; 2nd day, advanced segmentation; 4th and 5th days curved vermicules (the stage figured by Leuckart, *Menschl. Parasit.*, II. pt. 2, p. 213, fig. 8); 7th day, plump vermiform embryos; 8th day, active embryos.

The intermediate host of A. mystax.

Ripe eggs were administered to mice in their food. The details of the experiments are given below. Active *Ascaris* larvae were found in the liver between the 1st and 3rd days after infection. In Experiment 1 the eggs given on the 9th July were probably not old enough to be infective. The material at my disposal was unfortunately not large.

Expt. 1. 9th July. Mouse *N* given eggs of *A. marginata* 6 days old containing vermiform embryos.

12th July. Eggs of *A. marginata* 9 days old and of *A. mystax* 12 days old.

13th July. Eggs of *A. marginata* 10 days old.

14th July. Mouse *N* killed. No larvae in lungs or liver.

Expt. 2. 14th July. Mouse *P* given eggs of *A. marginata* 11 days old.

15th July. Mouse died 20 hours after infection. Eight larvae found in a portion of the liver, none in the lungs.

Expt. 3. 29th July. Mouse *U* given eggs of *A. marginata* 26 days old.

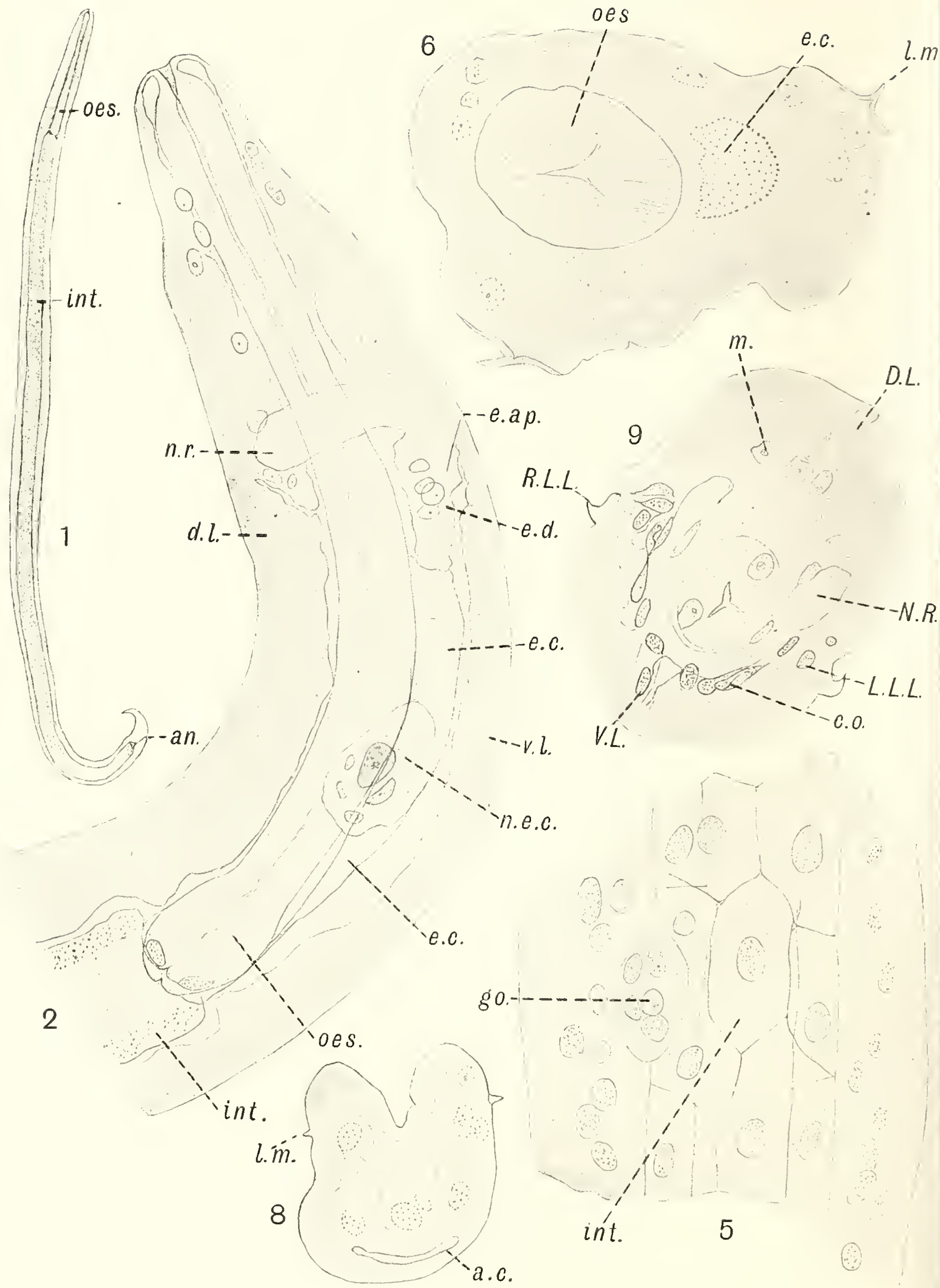
30th July. Killed. Larvae in the liver, none in the lungs.

Expt. 4. 29th July. Mouse *V* given eggs of *A. marginata* 26 days old.

1st August. Killed. One larva found in the liver, none in the lungs.

Expt. 5. 4th August. Mouse *Z* given a small dose of eggs of *A. marginata* 32 days old.

9th August. No larvae in lungs or liver.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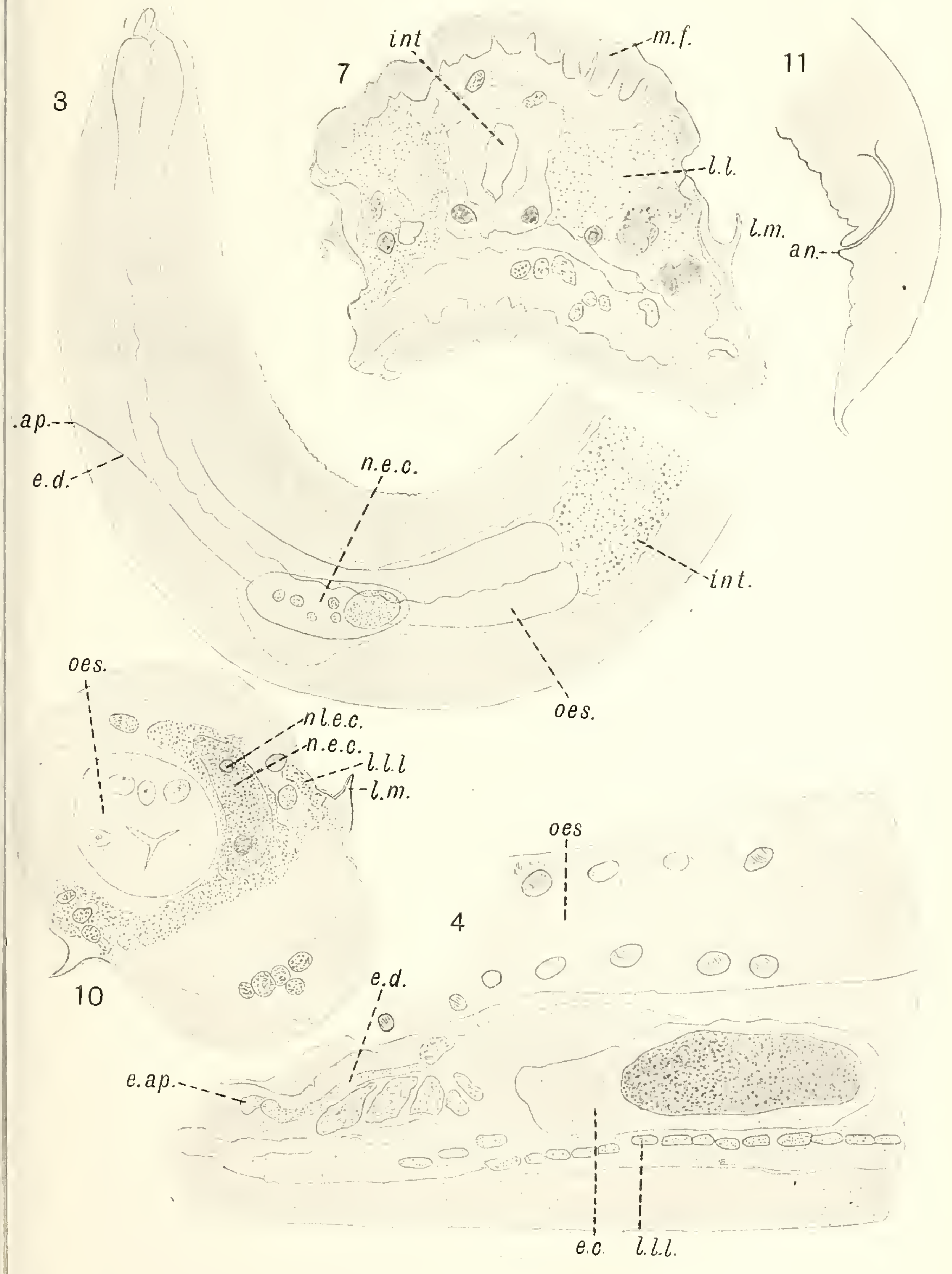
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Measurements of larvae of Ascaris marginata *from the liver of the mouse.* The specimens were killed by heat in salt solution. Larva 20 hours after infection. Total length, 0·38 mm.; oesophagus length, 0·122 mm.; relation of length of oesophagus to total length, 1 to 3·11; maximum breadth, 0·017 mm. The length and breadth are practically the same as in the embryo, the oesophagus has shortened markedly.

Larva on the third day after infection. Total length 0·42 mm.; oesophagus length, 0·130 mm.; length of oesophagus to total length, 1 to 3·23.

EXPLANATION OF PLATE IV.

Fig. 1. *Ascaris suilla*, larva from the caecum of the mouse, 12th day after infection. × 80.

Fig. 2. Anterior portion of larva from the small intestine of the mouse, 10th day. × 800.

Fig. 3. Anterior portion of larva from the faeces of the mouse, 11th day. × 800.

Fig. 4. Excretory gland and duct of larva from the large intestine of the mouse, 11th day. Seen from a point on the prolongation of the radius midway between the dorsal and left lateral radii. × 1360.

Fig. 5. The rudimentary gonad in a larva from the bronchi of the mouse, 9th day, × 1360.

Fig. 6. Transverse section through a larva from the caecum of the mouse, 11th day. level of the excretory gland. × 1360.

Fig. 7. Transverse section of a larva from the faeces of the mouse, 11th day, level of anterior end of intestine. × 1360.

Fig. 8. Transverse section of a larva from the caecum of the mouse, 11th day, immediately in front of the anus. × 1360.

Fig. 9. Transverse section of a larva from the trachea of the mouse, 9th day, level of the nerve-ring. × 1360.

Fig. 10. Transverse section of the same larva, level of the excretory gland. × 1360.

Fig. 11. *Ascaris suilla*, larva from the faeces of the mouse 10th to 11th day after infection Outline of the tail from the left side. × 689.

KEY TO LETTERING OF ILLUSTRATIONS.

a.c. anal canal; *an.* anus; *d.l.* dorsal line; *e.ap.* excretory aperture; *e.c.* excretory cell; *e.d.* excretory duct; *int.* intestine; *l.l.* lateral line; *l.l.l.* left lateral line; *l.m.* lateral membrane; *m.* muscle cell; *m.f.* muscle field; *n.e.c.* nucleus of excretory cell; *nl.e.c.* nucleolus of excretory cell; *n.r.* nerve ring; *oes.* oesophagus; *r.l.l.* right lateral line.

Table of Measurements.

(*Unless otherwise stated specimens were measured in normal salt solution.*)

		Total Length	Maximum Breadth	Length of Oesophagus	$\frac{\text{Length of Oesophagus}}{\text{Total Length}}$	Head to Nerve Ring	Anus to Tail	$\frac{\text{Post-anal Length}}{\text{Total Length}}$
Embryo 26 days in water		·28	—	·087	$\frac{1}{3\cdot3}$	—	—	—
(Following all from Mice)								
Larva from Liver	6th day	·735	·034	·14	$\frac{1}{5\cdot2}$	—	—	—
„ „ Lung	6 „	·70	·032	·148	$\frac{1}{4\cdot7}$	—	—	—
„ „ Trachea	11 „	2·10	—	—	—	—	—	—
„ „ Bronchus	12 „	1·90	—	·269	$\frac{1}{7}$	—	—	—
„ „ Trachea	13 „	2·07	—	—	—	—	—	—
„ „ Small Intestine	10 „	1·61	—	·22	$\frac{1}{7\cdot2}$	—	·06	$\frac{1}{27}$
„ „ Large Intestine	10 „	1·58	—	·23	$\frac{1}{6\cdot8}$	—	·062	$\frac{1}{25}$
„ „ Caecum	10 „	1·65	—	—	$\frac{1}{7}$	—	—	—
„ „ Large Intestine	11 „	2·10	—	·32	$\frac{1}{6\cdot6}$	—	—	—
„ „ Caecum	12 „	2·02	—	·3	$\frac{1}{6\cdot7}$	—	—	—
„ „ „	13 „	2·00	—	·3	$\frac{1}{6\cdot6}$	—	—	—
„ „ „	„ „	2·20	—	—	—	—	—	—
„ „ „	15 „	2·20	—	—	—	—	—	—
„ „ „	„ „	1·75	—	—	—	—	—	—
„ „ „	„ „	2·37	—	—	—	—	—	—
„ „ Faeces	10 „	1·40	—	—	—	—	—	—
„ „ „	12 „	1·60	—	·19	$\frac{1}{8}$	—	—	—
„ „ „	„ „	1·15	—	—	—	—	—	—
„ „ „	13 „	1·47	—	·2	$\frac{1}{7\cdot3}$	—	—	—
„ „ „	16 „	1·50	—	—	—	—	—	—
(Following from specimens in Canada Balsam)								
Larva from Trachea	9 „	1·36	—	·17	$\frac{1}{8}$	—	·046	$\frac{1}{30}$
„ „ Caecum	10 „	1·25	—	·163	$\frac{1}{7\cdot6}$	—	·061	$\frac{1}{20}$
„ „ Small Intestine	„ „	1·30	·052	·175	$\frac{1}{7\cdot4}$	·063	·049	$\frac{1}{26}$
„ „ Large „	11 „	1·50	·073	·23	—	—	—	—

ON THE LIFE HISTORY OF *ASCARIS LUMBRICOIDES* L.[1]

By F. H. STEWART, M.A., D.Sc., M.B., Major, I.M.S.

On *Ascaris* infection in Man and the Pig.

I. In the following three experiments it will be shown that ripe eggs of *Ascaris suilla* can hatch in the intestine of the pig, that the larvae issuing from these eggs enter the body of the pig and pursue the same course through the body as in the rat and mouse. They have been found in the lung of the pig from the 6th to the 8th day and in the trachea on the 8th day. Dead larvae have been found in the faeces of the pig on the 11th day after infection (Expt. 6).

Expt. 1. Sucking-pig No. 8, 20. II. 17. Nine days old, was given a very large dose of eggs of *A. suilla* 4 months old. The pig was killed, 26. II., and the pleura was found studded with small patches of ecchymosis, *Ascaris* larvae were present in these patches and throughout the lungs in large numbers, no larvae were found in the liver. No other organs examined.

Expts. 2 *and* 3. Sucking-pigs Nos. 6 and 7. On 20. II., nine days old, given very large doses of eggs 43 days old. On 26. II. both pigs were suffering from severe dyspnoea and cyanosis. On 28. II.–1. III. both pigs died during the night.

Ascaris larvae were present in enormous numbers in the lungs and trachea, 200 specimens were counted in a watchglass in which a fragment of trachea 1″ long had been dipped.

II. It may be assumed that any development undergone by *A. suilla* in the pig will also be undergone by *A. lumbricoides* in man.

[1] This paper is a continuation of work published in the *British Medical Journal*, July 1st, Oct. 7th, Dec. 2nd, 1916, and in *Parasitology*, IX. 155. The cost of the animals used in the experiments was very kindly borne by the Government of Hong Kong and the work was conducted in the Bacteriological Institute of that colony. My thanks are due for this assistance, and I am also indebted to Dr Johnson, P.C.M.O., Hong Kong, Dr Macfarlane, Government Bacteriologist and Mr A. Gibson, Colonial Veterinary Surgeon, Hong Kong, for the interest they have taken in the research.

The author regrets that he is obliged to publish incomplete work and pleads in excuse that he has been obliged to discontinue the research, not knowing when he will have an opportunity of resuming it.

That this assumption is correct is also proved in a remarkable manner by an experiment performed by Mosler (1860, as cited in Leuckart's *Menschl. Parasit.* II. pt. 1. p. 222, from the original paper in *Arch. Path. Anat.* XVIII. 249). Mosler, after a preliminary and negative experiment on himself, administered ripe eggs of *A. lumbricoides* to a number of children, at first in small numbers, but later several dozen to each child. No worms were at any time evacuated after anthelminthic treatment but in one (or two) of the children, fever with dyspnoea occurred a few days after the administration of the eggs. Leuckart adds that it is of course doubtful whether this fever was due to the experiment. There can now however be little doubt that the fever and dyspnoea were due to pulmonary ascariasis, the dose in one or two cases having probably exceeded several dozen[1].

III. We are then to consider the following facts, that ripe eggs of *A. lumbricoides* or *suilla* hatch in the intestine of their definitive hosts man or the pig, and also in the rat and mouse, and develop in the body of man and of these animals in an identical manner up to the 2 mm. larva in the trachea. Further that in the mouse the larvae then pass through the alimentary canal unharmed and are evacuated in the faeces.

To cover these facts two hypotheses may be advanced: (*a*) That the normal development of the worm occurs in one host only, the definitive host, man or the pig, and that the larvae in the trachea of man or the pig pass through the oesophagus and stomach and become adult in the intestine and that the development in the rat and mouse is merely an accidental development in an abnormal host and is unconnected with the life history of the parasite. This hypothesis was advanced in an Editorial in the *British Medical Journal*, July 1st, 1916. (*b*) That the rat and mouse are intermediate hosts and that the larvae passed in the faeces of these rodents can, either at once or after further development, infect the definitive host. On this hypothesis it may or may not be necessary to assume that the larval development in man and the pig is accidental. It is conceivable that the definitive host is able to act as an (unusual) intermediate host in addition to and in substitution for the usual intermediate (the rodent).

The former hypothesis is the simpler. It should be susceptible of proof or disproof by a moderately numerous series of experiments performed in the light of the facts I have established, the experiment being

[1] It is difficult to understand why Mosler should have selected the human child as a subject for experiment in place of the pig. The use of the latter appears preferable both from the practical and moral standpoint.

directed of course to ascertain whether after an infection in the pig in which *Ascaris* larvae are known to have reached the lungs, adult worms are found in the intestine after the lapse of a suitable interval. Now since the larvae cannot be demonstrated in the lungs without putting an end to the experiment, what criteria can be employed to judge of their presence in that situation? (1) The appearance of symptoms of pneumonia between the 7th and 10th days after the administration of the eggs may be regarded as proof positive. (2) Pulmonary infection appears to follow so constantly on the administration of an active culture of eggs both in rodents and in the pig, that if a culture is proved infective for a mouse it may be assumed that it will prove equally so for the pig.

Six experiments of this kind were performed by me (Expts. 4–9). In two of these the pigs undoubtedly suffered from *Ascaris* pneumonia (Expts. 6 and 8). In one there was also some evidence of this condition (Expt. 7). The culture used on two of the remaining three was proved active on mice (Expts. 4 and 5), while in the remaining case four different cultures were employed, the eggs in each containing active embryos (Expt. 9).

Results. In four of these animals (Expts. 4, 5, 8, 9) no worms were found in the intestine on section (with the exception of Expt. 8, in which one small *Ascaris* was found which was certainly not connected with the experiment performed several months previously). In one (Expt. 6) although a large number of worms were found it is probable that they did not originate in the experiment. In one (Expt. 7) a number of worms were found which may have originated in the experiment, but which may also have arisen from accidental infection. Comparing the measurements of the worms in Expts. 6 and 7, and the period which elapsed between the administration of the eggs and the finding of the worms in the two cases it is clearly not possible that the worms in both Expts. 6 and 7 originated from the eggs that were given. Out of the six experiments therefore five are negative, and one only possibly positive. Considering the very large number of larvae which must have reached the intestine, more than a thousand in each case, and the regularity and certainty with which the hepatic-pulmonary infection follows the administration of eggs in both the rat, mouse and pig, the evidence of these six experiments is opposed to the hypothesis of direct development without an intermediate host. Nevertheless six experiments are not sufficient to decide the matter and it must therefore still be considered unsolved.

Expt. 4. Sucking-pig No. 9. On 28. II. 17, when eleven days old, it was given a moderate dose of eggs $2\frac{1}{2}$ months old, the culture had previously been proved infective to mice. On 14. III., it was killed, the stomach, small intestine and caecum were thoroughly washed out separately, the washings being repeatedly sedimented and rewashed, and finally examined on a dark surface; no worms were found. I am certain that no worm over 2 mm. in length would have escaped my observation.

Expt. 5. Sucking-pig No. 10. On 28. II., when eleven days old, it was given a small dose of the same culture as Pig 9. On 20. III. it was killed, but no worms were found in the intestine.

Expt. 6. Pig No. 11. On 28. II., when $2\frac{1}{2}$ months old, it was given a large dose of culture 3 months old. On 9–10. III. it was suffering from marked dyspnoea and cyanosis; the temperature rose to 105° F. On 11. III. it had recovered, two dead and partially macerated *Ascaris* larvae being found in the faeces; the latter loaded with unsegmented *Ascaris* eggs. On 20. III. it was killed, and 38 ♀ and 19 ♂ *Ascaris* were found in the intestine, measurements of the females in mm. were: 250 (2), 220 (2), 210 (3), 205 (1), 200 (1), 190 (1), 180 (1), 172 (1), 170 (3), 165 (4), 155 (5), 145 (4), 140 (3), 135 (2), 125 (2), 105 (1), the bracketed figures denote the number of specimens of each measurement. The males measured between 160 and 65 mm.

By way of commentary on the above I would note that the measurements form a fairly continuous series with the maximum numbers at the medium measurements, 145–170 mm. in 18 specimens. This suggests that the worms emanated from several infections that closely followed each other. It does not suggest an infection 20 days old superposed on one at least 50 days old. Also if these worms originated in the experiment it is necessary to suppose that a larva of 2 mm. grew to a worm of at least 105 mm. in 10 days.

Expt. 7. Pig No. 12. On 28. II., when $2\frac{1}{2}$ months old, it was given a dose of eggs 3 months old, rather fewer than were given to Pig 11; the culture had proved infective to mice. On 7. III. the animal was slightly dyspnoeic, its temperature 103° F. (normal 102·6° F.). On 30. III. it was killed and 22 *Ascaris* were found in intestine, their sex not being ascertainable from tail character. The measurements, in mm., were 70, 60, 45 (2), 42, 40, 37, 35 (2), 33 (4), 31 (2), 30 (2), 28, 27, 25, 20.

I would note that these young forms may have originated from the eggs administered 30 days previously. Comparing their measurements with those of the worms from Pig 6 it is clear that if any of the former originated from the experiment none of the latter did and vice versa.

Expt. 8[1]. Pig A. On 20. IX. 15, when aged 2 months 20 days, it received a small dose of *A. suilla* eggs. On 21. IX.–23. IX. the doses were repeated daily. On 13. X. 15 it received large doses of eggs 57 and 64 days old. On 19. X. the pig's respirations were rapid. On 20. X. it showed marked dyspnoea and fever lasting until 23. X. On 24. X. it recovered. On 15. XII. the faeces having been repeatedly examined and no eggs found, it was killed, and I found one *Ascaris*, measuring about 80 mm., in intestine.

[1] See footnote p. 201.

The attack of pulmonary congestion was not recorded previously as I believed it was unconnected with the experiment.

Expt. 9[1]. On 27. IX. 15, the pig being 2½ months old, from this date to 2. XII. it received repeated doses of eggs of human *Ascaris* but no eggs appeared in the faeces. On 5. I. 16 eggs of *Ascaris* of the pig, 68 days old, were given. On 10. I. ditto, 73 days old. On 18. I. ditto, 20 days old. On 5. II. ditto, 17 days old. On 23. II. no eggs were found in the faeces. On 27. II. eggs 39 days old were given. On 27. III. no eggs occurred in the faeces. On 30. IV. the pig was killed and no ascarids found.

EXPERIMENTS ON THE INFECTION OF PIGS WITH THE LARVAE FROM MICE.

In these experiments it is difficult to obtain a sufficient number of *Ascaris* larvae from the caecum of the mouse since if large doses of eggs are given to the mouse the animal dies before the 9th day, while if small doses are given only very small numbers of larvae are found in the caecum.

Expt. 10. Sucking-pig No. 1. On 28. I. 17, when 4 weeks old, its faeces were examined and no *Ascaris* eggs found. The caeca of 4 mice, on the 10th day after infection, were given to the pig; the mice were known to be infected. On 11. II. the pig was killed, 12 *Ascaris* were found in its intestine, 2 large, most anterior (a ♂ 124 mm., a ♀ 183 mm.), 10 smaller worms further back measuring 73, 70, 65, 64 (2), 63, 60, 47, and two ♂♂ 61 and 55 mm. respectively.

Expt. 11. Sucking-pig No. 2. On 28. I., when 6 weeks old, it showed no eggs in the faeces. The caeca of three mice on 10th day after infection were given. On 11. II. the pig was killed, and no *Ascaris* were found present.

Expt. 12. Control on Expt. 10. Sucking-pig from same farrow as Pig 1. It was killed and no *Ascaris* found.

Expt. 13. Control on Expt. 11. Sucking-pig from same farrow as Pig 2. On 15. II. it was killed and 12 *Ascaris* measuring 207–119 mm. were found. This detracts from the importance of Expt. 10.

EXPERIMENTS TO OBTAIN *ASCARIS* LARVAE IN THE CAECUM OF THE MOUSE.

The difficulty alluded to above must be borne in mind.

A series of 46 mice was employed. Of these (*A*) four were examined without treatment. No forms resembling *Ascaris* larvae being found.

(*B*) Ripe *Ascaris* eggs were administered to 42 mice with the following results: sixteen died before the date of examination with the usual symptoms of acute Ascariasis; six were not examined, the organs being given unopened to pigs; six were not examined from other reasons.

[1] Previously recorded in *Brit. Med. Journ.* 1. VII. 1916, and *Parasitology*, IX. 155.

Nine were examined on the 10th day. *Ascaris* larvae were found in the caecum in five, in the lungs and trachea but not in the caecum in one, and three were negative.

Five were examined on the 11th day. Larvae were found in the caecum in one, in the lungs and trachea but not in the caecum in two, and two were negative.

Anatomy of the Larvae of *A. suilla* from the Pig.

Unfortunately I was unable to take detailed measurements of many specimens owing to lack of time. The only difference noted, compared with larvae from rodents, consists in the fact that the excretory gland lies slightly further back, the nucleus being on a level with the posterior end of the oesophagus.

The following are the measurements of a specimen on the 8th day from the lung, fixed by heat in salt solution. Length 1·5 mm., oesophagus 0·23, oes./length 1/6·5.

Measurements of specimens from lung of pig on the 6th day (1) Total length 1 mm., maximum breadth 0·038, oesophagus length 0·176, oes./t.l. = 1/5·6. (2) T.l., 1 mm., br. 0·038. (3) T.l. 0·8 mm., oes. 0·15, oes./t.l. = 1/5·3.

Note. Correction of the description of the larvae from rodents in *Parasitology*, IX. p. 155.

The excretory gland can be identified in larvae as young as that figured in Pl. I, Fig. 2 (from liver of mouse 2nd–4th day). Even at this early stage it lies in the same position as later, in the left lateral line opposite the posterior swollen portion of the oesophagus. The orientation of Figs. 6 and 7, and 9–12, Pl. I, is therefore incorrect. The letters *VL.* should read left lateral line, the lines marked *L.L.* are the median lines, and *D.L.* is the right lateral.

Economic importance of Ascariasis in Pigs.

Regarding the prevalence of ascariasis infection in pigs, Lynch (*Diseases of Swine*) states that "in the large packing houses of Chicago, Kansas City and Omaha the parasites are found in large numbers in nearly half of the animals slaughtered." My friend Mr A. Gibson kindly made an estimate of the proportion of animals infected among those slaughtered at the West Point abattoir, Hong Kong, and informed me that at least 50 % were infected. I examined 83 pigs from the Hong Kong dairy farm and found 24 % infected. The animals on this farm are kept under exceptionally sanitary surroundings and it might be expected that the infection would be low.

As to the effect of the disease on the individual animal I would note the following: of the above 83 animals 44 were classed as doing well, 39 as doing badly. In the former group 11·3 % were infected, in the latter 33·3 %.

Pulmonary Ascariasis in pigs: I am informed on good authority that pneumonia is a common disease of young pigs and that a pig which has suffered from pneumonia is considered unthrifty and slaughtered forthwith to save waste in feeding. A certain number of these cases may be due to Ascariasis.

The loss of valuable food material through Ascariasis in pigs may therefore be considerable and of great importance at times of food scarcity such as the present.

IMPORTANCE OF ASCARIASIS IN MAN.

Pulmonary Ascariasis in Man. It may be doubted whether under natural conditions man would ever receive a sufficiently large dose of eggs to cause serious pulmonary symptoms in a healthy person. The injury caused to the lung by the passage of the larvae might readily be the starting point of bronchopneumonia in a weakly child. The passage of the larvae may also be the cause of many of those irregular febrile attacks which are common in children in districts in which *Ascaris* is common.

The cosmopolitan distribution, great prevalence and debilitating results of intestinal Ascariasis are old-established facts. It may be doubted, however, whether the importance of the disease in state medicine is sufficiently recognised. There is reason to suppose that a great deal of the debility of the natives of the tropics is due to Ascariasis and that this disease is at least equal to Anklylostomiasis in economic importance.

DEVELOPMENT OF THE EGGS OF *ASCARIS LUMBRICOIDES* IN VARIOUS MEDIA[1].

(1) *In Human Faeces.*

Development of the eggs, up to an advanced stage of segmentation can take place in human faeces when freely exposed to the air (Expts. 1 and 2 v. infra), but it is considerably slower and more irregular than in damp air. On the third day after evacuation, the eggs are still

[1] I regret being unable to refer to the recent literature of this subject, therefore I cannot ascertain if similar observations have already been made or not.

largely unicellular, but some 2–6 cell stages occur. On the 7th day the eggs are in advanced segmentation. No experiment was conducted with eggs in human faeces placed on the ground as in Expt. 8 with pigs' faeces. The rapidity and extent of development is determined by the degree of aeration and dampness of the nidus (Expts. 2–6). Eggs of *Ascaris lumbricoides*, which remain in human faeces, do not lose their power of full development on removal to a more favourable nidus. It is therefore probable that they could complete their development in human faeces lying on the ground in the open air.

(2) *In the Faeces of the Pig.*

Full development can take place in the faeces of the pig when completely exposed to the air and kept moderately damp (Expt. 8). In this nidus development is as rapid as in the case of eggs washed and kept in a damp atmosphere. Fully developed embryos are found on the thirteenth day after evacuation.

(3) *In contaminated Water.*

Numerous observations were made on eggs washed out of human faeces and kept in the contaminated water. In no case was any development observed.

(4) *In uncontaminated Water.*

Eggs removed directly from the uterus and placed in tap water can reach full development, but as Leuckart pointed out development is extremely irregular in point of time and a large proportion of the eggs undergo no development whatever.

(5) *On the surface of the Soil.*

In nature, conditions of thorough exposure to air and dampness, without actual immersion in water, are found in the superficial layers of the soil. Eggs of *A. lumbricoides*, removed directly from the uterus, and placed on the surface of moist clayey earth, were found to reach the vermicule and early vermiform embryo stages on the tenth day, and the stage of fully formed embryo on the twelfth day, the temperature and humidity being that of Hong Kong in the summer: 80–90° F. and humidity about 90 %.

Experimental Records relating to the development of the Egg of A. lumbricoides *in Human Faeces.*

	Date	Day	Nature of experiment and result of examination
Expt. 1.	21 VIII	0	Stool containing eggs placed in an open bowl covered with wire gauze in the open air
	24 ,,	3	Eggs mostly unicellular. Few irregularly segmented.
	27 ,,	6	Eggs in condition of advanced segmentation.
	31 ,,	10	No signs of further development—many degenerated.
Expt. 2.	21 ,,	0	Eggs washed out of the same stool as used for Expt. 1, and placed in a damp atmosphere.
	1 IX	11	Eggs contain vermiform embryos.
Expt. 3.	21 VIII	0	Same stool as in Expt. 1.
	22 ,,	1	Ditto.
	23 ,,	2	Eggs washed out and kept in foul water.
	24 ,,	3	Eggs transferred to a damp atmosphere.
	1 IX	11	No development of eggs.
	13 ,,	23	Eggs contain vermiform embryos.
Expt. 4.	21 VIII	0	Same stool as in Expt. 1.
	24 ,,	3	Eggs washed out and placed in a damp atmosphere which became foul smelling.
	1 IX	11	1–2–4-cell stages and stages of more advanced segmentation.
	2 ,,	12	Transferred to a damp atmosphere; not foul smelling.
	13 ,,	23	Eggs contain vermiform embryos.
Expt. 5.	21 VIII	0	Same stool as in Expt. 1.
	27 ,,	6	Eggs washed out and placed in a damp atmosphere.
	31 ,,	10	4-cell stages to curved vermicules.
Expt. 6.	21 ,,	0	Same stool as in Expt. 1.
	31 ,,	10	Eggs washed out and placed in damp atmosphere.
	13 IX	23	Eggs: some unsegmented, some with curved vermicules, some with vermiform embryos.
Expt. 7.	24 VIII	0	Faeces containing eggs in open bowl covered with wire gauze in open air.
	27 ,,	3	2–6-cell stages.
	4 IX	11	Faeces dried. Eggs degenerated.

Development of the Egg in the Faeces of the Pig.

	Date	Day	Nature of experiment and result of examination
Expt. 8.	19 VIII	0	Faeces of pig containing eggs placed on squares of card-board on the ground and covered with perforated tins.
	24 ,,	7	Eggs in condition of advanced segmentation.
	26 ,,	9	Eggs contain curved vermicules.
	1 IX	15	One specimen has become very wet from heavy rain, almost all the eggs are degenerated. Another specimen has remained only moderately damp, eggs contain vermiform embryos.

SOME RESULTS OF A SURVEY OF THE AGRICULTURAL ZOOLOGY OF THE ABERYSTWYTH AREA.

By CHAS. L. WALTON, M.Sc. (Wales).
(*Departments of Zoology and Agriculture, University College of Wales, Aberystwyth.*)

During the period 1913—16, I conducted a Survey of the Agricultural Zoology of the Aberystwyth Area, for which purpose the University authorities received a grant from the Board of Agriculture. The area thus examined comprised N. Cardiganshire and some adjacent borders of Montgomeryshire, roughly about 250 sq. miles. It falls into three main physical divisions:

I. The mountainous upland (or high plateau) of solid rocks frequently covered by a considerable depth of peat. The rock succession is only irregularly exposed in deep stream cuttings, while these valleys are occupied by boulder clay and river deposits.

II. The surface of the coastal plateau shows exposures of rock and of boulder clay. The clay is usually exposed and rarely covered with peat.

III. The fall line, which is intermediate. Here the boulder clay generally follows the valleys, and it is usually covered with a thin layer of peat. Much of this is readily cut through by small streams.

The Dyfi Flats (or Borth Bog) form a distinct type consisting largely of peat but with a few well-defined tracts of tenacious clay (alluvium). To the south-east of the area are large districts floored entirely by boulder clay, and ill-drained.

The high plateau is the great summer grazing area for sheep; the fall line or slope between it and the lower coastal plateau is of considerable extent and importance and includes much of the woodland of

the area; this land is frequently rough and ill-drained, and the numerous streams traversing it often occupy deep ravines or cwms. The coastal plateau contains the best cultivated agricultural land, and also, naturally, the bulk of the population. The chief rivers of the Area are the Dyfi (the estuarine portion of which bounds Cardiganshire to the north and receives a number of mountain streams) the Rheidol and the Ystwyth, while to the south-east the watershed of the Teify is reached.

The rainfall of the whole Area is considerable, increasing as the mountains are approached, and varying from 31 to 42 inches at Aberystwyth, 41 to 56 at Gogerddan and 48 to 70 at Hafod (near Devils Bridge), while Plynlymon receives from 90 to over 100 inches annually. From the point of view of the Agricultural Zoologist the area surveyed is divisible into six chief divisions, each with its own typical pests and diseases, varying with the elevation, type of soil, amount of rainfall, degree of cultivation and population, and kind of stock predominating. Much of the Area is rough and relatively inaccessible, and the examination of the sheep walks, etc. entailed a very considerable amount of arduous walking, especially during the winter. Throughout the Survey first place was given to field work, and in all some 250 different farms and holdings were visited, and as a rule examined.

In general the farming does not reach a high level, the character of the land and climate in many cases being adverse, and the farm buildings frequently sadly inadequate, though there are, of course, a number of notable exceptions to the above general statements. Sheep farming and cattle rearing naturally predominate; agriculture being chiefly accessory. In addition to the parasites and pests described, some details of the local sheep farming, etc. are given.

GID (*MULTICEPS MULTICEPS*).

This disease is one of the most troublesome to sheep farmers within the Area, and though rarely the cause of heavy losses, is a constant source of annoyance. Considerable attention has been given to the matter of its distribution, etc. and in order to understand its occurrence it is needful to make a short résumé of the various types of sheep farming practised within the Survey Area and the adjacent country.

The Area is a wide one and comprises very diverse types of country, roughly divisible as follows:

(*a*) Salt marsh } Dyfi Flats.
(*b*) Lowland peat bog }

(*c*) Lowland arable and pasture land (Coastal Lowlands and Uplands).

(*d*) Wooded valleys (Fall Lands, etc.).

(*e*) Rough hillside arable and pasture (largely undrained).

(*f*) Upland peat bog } High Plateau.
(*g*) Upland sheep pasture }

All these possess their own types of sheep farming and peculiarities having a bearing on the distribution of this disease. Many farms have a very great vertical range and include several (or even all) of the above types; while others may be confined to one only.

The following are the more usual types of sheep farming:

1. Lowland farms keeping a standing ewe flock which never leaves the place.

2. Lowland farms keeping a standing flock, but sending all (or most) to some mountain "walk" for the summer.

3. Lowland farms merely taking in lambs to "Tack" for the winter months, either from mountain sheep walks within the Area; or from Brecon, Radnor, etc., the sheep being from one to several days on the road.

4. Lowland farms buying in a fresh (wholly or in part) flock each autumn.

5. Farms combining any of the above, and possibly, in addition buying in a lot of wethers to fatten for the butcher.

6. Farmers holding both upland and lowland farms, and working the sheep up and down as may be needful besides, perhaps taking in "Tack" sheep on both places for "wintering" and "summering."

7. Mountain sheep farms which:

(*a*) Keep wethers on the high hill all the year, until they are three or even four years of age, and send down the yearlings to the lowlands each winter.

(*b*) Sell their lambs out annually, keeping only a proportion of young ewes.

(*c*) Supply drafts of ewes to lowland flocks, and keep the wethers.

(*d*) Variously combine the above and take in lowland sheep for the summer, etc., etc.

The whole of the above may be modified in various ways. The chief results are the great seasonal movements of lambs into the Area for the winter, and out again six months later; and the equally great movements to and from the mountains, and from farm to farm. There are also considerable movements connected with fairs, with shearing, and with dipping. A detailed account of the local farming will be found in the forthcoming Report on the Economic Survey of the Aberystwyth Area by Mr J. Pryse Howell. Of the 250 farms and holdings from which data were obtained we may neglect 75 on which either no sheep were kept, only wethers were bought in to fatten, or the data obtained were unsatisfactory. This leaves 175 from which to draw conclusions, and these fall into three categories:

A.	Flocks always kept at home (no movement) ...	68
B.	Flocks from which sheep are moved only within the Area surveyed (short to medium movement)	77
C.	Flocks from which sheep are moved to places without the Area, or moved into the Area from without it (medium to long movement) ...	30
	Total ...	175

If these classes are now examined in turn, using the data given me by the farmers and shepherds, we discover differences in the degree of infection as follows:

A. Out of a total of 68 flocks only 15 complained of Gid (locally known as *Bendro*, from *pen* = head, and *tro* = turn, both words mutate and thus become *bendro*), and in all cases the infection was slight.

The percentage of infected flocks in this category is 22. Of the 15 flocks affected, seven had a mountain run adjoining, two were intersected by high roads (from which sheep are seldom effectively excluded), one grazed on an adjacent common, and another, in addition to a high road, walked hound puppies, thus increasing the number of dogs and the possibilities of infection. It is presumed that sheep grazing along a high road run increased risks of infection from grass fouled by dogs. No definite figures are available for these 15 flocks, "a case now and again" being usually reported; probably ·5 % would be fairly accurate.

B. Seventy-seven flocks come within this category and of these no less than seventy complained of Gid, or 90·9 % of the flocks. Many farmers were uncertain as to the actual number of cases and while complaining of trouble, stated "a few," "one or two," "several," or used

other equally vague terms; but for 18 out of the 77 flocks definite figures were given me, from which it appears that 1·64 % of the lambs and yearlings were affected; the usual being 1 to 1·5 % and the highest 4 % (in one flock).

C. Thirty flocks; affected 22, free 8. Two were but slightly infected, and out of the remaining 20, 12 furnished definite figures, working out at an average of 2·3 % of lambs and yearlings, the highest reported being 4·5 %. The percentage of flocks infected is 76·3.

The marked contrast between A on the one hand, and B and C on the other is at once apparent, and may be ascribed to one or more of three factors:

(1) summering on the mountains,
(2) wintering in the lowlands,
(3) travelling along the roads.

All the data for group C are not available, since in each case farms or sheep walks outside the Area are involved. In the case of lambs travelling into the Area in October for winter grazing the probability is that they were infected before they left their own farm or hill run. A certain number are generally too sick to travel back in the following April and remain, to die, on the lowland farms or fall out on the way. Some of these lambs come from considerable distances, Corris, Newbridge on Wye, Rhayader etc. in Radnorshire, many parts of Brecconshire, and even Carmarthenshire; and are two to three days upon the road, being put for the night into certain fields regularly used for this purpose; the reverse process occurs six months later. Considerable opportunity exists in these cases of infection taking place en route.

A few flocks, mostly in the northern part of the Survey Area "tack" lambs for the winter in the vicinities of Port Madoc, Criccieth and other places even further away. These lambs are sent by rail and not by road, yet Gid occurs among the flocks.

The best data are available for class B. In this instance the majority of lambs are born during March—April in the lowlands and are moved to the mountains in April and May; hence they naturally graze but little before leaving the lowlands: or, they are born upon the lower lands of the hill sheep walks and do not go to the lowlands until autumn. I have compared the data for both these groups and they point convincingly to the sheep walk as the chief source of infection. Although the range there is wide, yet the sheep speaking generally do not wander so much as might be imagined, and keep very largely to their own

portion of mountain, unless moved by the shepherd, and this applies particularly to the ewes and lambs. The number of dogs kept on the upland farms and sheep walks is often very considerable, and while one or two suffice for a lowland farm, six to ten are kept in the uplands. It stands to reason that the vicinity of the house and buildings or sheep pens will be much more fouled than is the case in the lowlands. Further, at such times as washing, shearing etc. the number of dogs brought together is often very large, and infected dogs may thus spread the disease in a number of places. The rainfall in the uplands is also much heavier than in the lowlands. It is my belief that infection takes place largely when the sheep have been gathered together about the house, the washing or dipping pens etc. especially after heavy rain or a wet period. This is supported by the number of pet lambs that contract gid, a matter of general knowledge. Many sheep-men state that gid is most in evidence after wet years. Gid in cattle seems largely to be confined to the sheep walks, where the beasts chiefly graze the limited area of improved land, usually near the house (though in summer they may range more widely).

Several men who kept stationary flocks free from gid and have subsequently taken mountain walks, have at once become troubled with the disease. There is often considerable irregularity in the number of cases occurring on any given holding in different years, and this may be influenced by the relatively wet or dry weather; but it is also affected by the number of young sheep, which varies considerably according to the weather experience during the lambing season. Adverse conditions may occasion heavy mortality, especially among flocks lambed at the higher elevations; other causes being equal, this would affect the number of cases in the following year. Cases have been reported to me from January to June, and in the latter month in 1916 one small flock lost two pet lambs from this cause. The majority of cases, however, are noted in March and April. A mountain farmer informs me that when he took over his present holding (the flocks are usually transferred with the tenancy) 16 years ago, no less than 40 cases of Gid occurred within the first twelve months. The precautionary measure of destroying all infected heads was adopted and the total reduced to twelve within a couple of years; one case now and again is the present extent of the trouble.

As far as treatment is concerned, extraction is commonly practised; many farmers own the necessary instruments and frequently operate for neighbours. The results vary with the operator, but on the whole

are favourable. There still remain, however, a considerable number of men who either pierce the skull at the softened area with a hot wire, or stab it with a pen knife or similar weapon; subsequently dressing the wound with tar. I have seen several complete recoveries after this rough treatment. Some others either kill very severe cases or simply allow the animal to die, and it is these men who perpetuate the disease and largely undo the good accomplished by those who systematically practise extraction.

Some strange ideas still exist in the mountains regarding the origin of gid. Sheep suffering from this disease almost invariably gravitate to the lowest levels, and then are not infrequently drowned in the streams that occupy the valley bottoms. I have been informed that the disease originates through certain sheep persistently grazing by the side of running water; the giddiness resulting from the brain being affected by the sound of the ever-flowing streams. A certain number of cases also called *bendro* locally are undoubtedly due to other causes, such as a blow on the head, but many such are recognised by the shepherds. Still it is possible that one or two such may have become included in my data, although precautionary questions were always asked.

One very significant fact remains. It will be noted that a considerably larger proportion of cases have been reported from the centre of the Area. These are the regions most hunted by the Gogerddan pack of foxhounds and in which the hound puppies are chiefly "walked." Since dogs are the distributors of gid, any increase in their numbers must tend to have an adverse effect, especially when these range widely over the country. It has been experimentally proved[1] that strong jawed dogs are the most active agent in spreading gid, owing to their greater ability to crack open the skulls of dead sheep and so become infected with the tape worm. The young hound is among the strongest jawed dogs of the Area, and I have met them on the mountains far from the farms where they were being reared. A number of cases of Gid in young cattle have been reported to me, practically all from sheep walks (as has already been mentioned) but despite my very numerous visits to these farms, I have not personally seen a case.

[1] M. C. Hall, "Methods for the Eradication of Gid," U.S. Bureau of Animal Industry. Circular 165. 1910.

Echinococcus veterinorum Sieb.

(*Taenia echinococcus*).

Cysts were obtained from the liver of a sheep that also contained a number of specimens of *D. hepaticum.*

Tape Worms of Sheep and Lambs.

Soon after the commencement of the Survey, a farmer from the neighbourhood of Aberystwyth complained that his lambs had not "done" well in the previous year, and judging by his description I believed tape worms were the cause. Enquiries at slaughter houses etc. elicited the information that these parasites were exceedingly abundant in a number of flocks within the Area, and that the farm above mentioned was heavily infected.

To have followed out all the details of this matter would have involved the expenditure of more time than could be spared from the other survey work, and Mr F. W. Flattely, then a research student in the Zoology Department of the University, commenced a careful study of the worms etc., using chiefly the farm already cited. Very promising and interesting results were being obtained when Mr Flattely left to take up a post under the International Institute of Agriculture, Rome, where he has, as far as possible, continued the study of *Moniezia.*

A good deal of material was collected from local slaughter houses, and from ewes and lambs that had died, and Mr Flattely, before he left, had obtained two species of *Moniezia* which he subsequently identified as *M. expansa* and *M. trigonophora,* and he also proved that both these species may occur in the same lamb.

To determine the relative distribution of these two forms in the Area would be a troublesome matter, and the close study of these pests would entail a separate and careful research.

Mr Flattely obtained as many as seventy-five individuals from a single lamb, and there is no doubt that these worms are the cause of a considerable loss to local farmers, especially those who feed lambs for the butcher. Ewes are also affected to some extent.

I continued to make inquiries and observations and obtained proglottides from droppings at a number of places in the Area from April to June, and gained a list of a dozen farms where the worms had been noted.

Examination of a number of sheep walks during May—June only resulted in the discovery of one lot of proglottides and that among lambs recently brought up from the lowlands (June 1915), and, so far, I am without positive evidence of these worms above 1000 ft., and the causes of presence and absence are still obscure. I have been told by some shepherds that they see the worms "now and again"; others have never noted them, while still others say "common." I have also received reports of tape worms from South Cardiganshire, Carmarthenshire and Pembrokeshire where they were said to be very abundantly seen in the slaughter houses.

Reports from Aberystwyth and local men state that lambs of only six weeks may be heavily infected with worms of great length; that lambs killed in autumn contain fewer worms and those much less in length; whilst in ewes the worms are comparatively rare.

Lambs from some farms appear to be always free. It is of course noteworthy that only lambs considered to be fat reach the slaughter houses, the worst cases being retained upon the farms. I have frequently observed enormous masses of *Moniezia* littering the floors of the abattoirs and noted the eager manner in which poultry will eat them. It seems very desirable that these species of *Moniezia* should be carefully investigated and the Aberystwyth Area would be very suitable for such work.

"Husk" (Verminous Bronchitis).

Forty farmers complained to me of "Husk" and though I feel certain that a number of these cases were caused by the Nematode *Strongylus filaria* I would not like to affirm that this parasite was the cause of them all.

Most of the complaints came from farms situated on damp or clayey land, and in many cases the calves had been allowed to graze in a field containing an undrained or swampy patch, or one in which the drains had become blocked, this causing very similar conditions. It is worthy of note that during a drought, calves are not infrequently allowed to graze aftermath near streams, etc. or in low lying fields where the growth of grass has continued, while the fields usually used for calves have become very bare. As a result of this, husk is reported from these farms while others are free. Those farmers who take precautions and care, who keep their calves indoors until the sun has dried the grass and away from swampy land, etc. and adopt other reasonable means, seldom have cause for complaint. In one case, on the Dyfi Flats, where

frequently it is by no means easy to find a really dry place for calves, an unusually high tide caused much of the land to be flooded with brackish water; and there has since been a marked diminution in the amount of husk. In another instance turning the calves into a field regularly "salted" thus, results in a cure. One farmer, the whole of whose small farm is very damp, keeps his calves on the shortest grass available. Calves sent from a dry farm to a damp common in Aug. 1915 became very badly infected.

It may not be out of place to state here that all my observations go to prove that Commons are great breeding grounds for parasites, and are centres of infection wherever they exist. I have traced "husk" and "red water" to one common within the Area, and liver rot to three others, one within, and two others just without the boundaries. The same thing applied to other parts of England and Wales.

These Commons are not drained, the weeds are not cut; the ponds and ditches are not cleaned out, everything is grazed off them and nothing returned, and they become poor, sour and foul; ideal centres for the maintenance and distribution of pests of all kinds: and it is greatly to be hoped that the future will see some efficient control of commons. Local husk remedies commonly in use are: sulphur and milk, tar and turpentine; balls compounded of linseed; turpentine and tar, or a tar ball dipped in turpentine.

Syngamus trachealis Siebold.

The Gape Worm is a serious chicken pest on a number of farms, often causing heavy mortality in April, and even as early as March, is by no means a general pest and is of quite local occurrence. Forty to sixty chicks have died in some instances that came under my notice; a loss by no means easy to replace. In several instances the removal of the rearing pens to fresh ground has been completely successful; no further cases occurring.

Experiments in painting the trachea in badly infected chicks with varying strengths of alcohol, dilute formalin, etc., were not successful. A number of fumigants, powders, etc., have been tried locally with varying results, but the disease is best combated by clean ground and disinfection.

Several people within the Area are expert at extracting the worms by means of a feather.

Ascaris suilla.

This large worm is commonly met with in the local slaughter houses, and is said to be more abundant in pigs that have had their liberty and have had the run of fields and yards prior to feeding, than in those that have always been penned and artificially fed.

Ixodidae.

Five species of ticks have been collected, namely:

1. *Ixodes ricinus* (L.).
2. *I. hexagonus* Leach.
3. *I. canisuga* Johnston.
4. *I. unicavatus* Neumann.
5. *Dermacentor reticulatus* Fabricius.

Of these, *I. ricinus,* as the undoubted carrier of bovine piroplasmosis is easily first in importance, and is also extremely abundant throughout the Area, especially among rough herbage, near woodlands, etc. Females, in all stages of engagement are frequently seen in abundance upon cattle and I have commonly taken them upon farm dogs, generally above the eye or about the ear, and I have on several occasions found the male in copula in such situations.

This species also occurs upon sheep, and I have handled considerable numbers in varying parts of the Area in order to note their presence, since shepherds and flock owners almost invariably confuse ticks and "keds" (*Melophagus ovinus*) and their evidence could therefore very seldom be relied on. I have only taken *I. ricinus* from mountain sheep and never abundantly. During mid-June, 1915, I found nymphs attached to the noses of about one-quarter of a large flock that had been grazing the natural pastures north-east of Talybont (900—1500 feet), but only one adult female was found, attached to the ear. Females were also taken several times from fox and cat, and specimens were sent me from hare and squirrel, these latter were nymphs and were obtained near Goginnan.

I have several times taken larvae from the skin of human beings (including myself) and I have had a number of complaints from agricultural workers, fern cutters, and others.

In March 1914, Messrs Hutchings, the Aberystwyth taxidermists (to whom I am indebted for many ticks and other interesting specimens)

sent me a number of "cysts" taken from beneath the ear, and about the groin of two foxes killed in the south of the Area. On opening one a tick was found within, and the whole were forwarded to Prof. G. H. F. Nuttall, F.R.S., who identified them as *I. ricinus* (♀) and *I. hexagonus* nymph. A note by Prof. Nuttall describing these specimens appeared in *Parasitology*, VII. p. 258. He says "This appears to be the first case of the kind recorded in Gt. Britain," and concludes "The penetration of *Ixodes* beneath the skin is not due to mechanical activity on the part of the tick. It is due to the increasing oedema and inflammatory swelling of the host's skin whose surface rises above the subjacent tissues in which the tick's hypostome is anchored—while the tick is sucking the host's blood, the host's skin revenges itself by swallowing the tick. After the tick has penetrated beneath the skin, the wound it produced may heal and be obliterated. The long hypostome of *Ixodes* appears to be an essential factor in the process, for we have no records of *Ixodidae* with short hypostomes penetrating beneath the skin.

However long the ticks may live in this situation, the firm cyst-like mass of tissue which forms above them necessarily renders their subsequent escape impossible and they must die *in situ*." Further specimens from foxes have been obtained. *I. hexagonus*, this species has been obtained (in addition to the above-mentioned record) from polecat, ferret, badger, and otter. It is common upon the two former. The very rare male was taken from the badger while from the otter one female and three nymphs were obtained (June 1916).

I. canisuga, one female from a badger.

I. unicavatus, several specimens from a shag.

D. reticulatus has been taken crawling upon a dog that wandered about the rough hill known as Pen Dinas, close to Aberystwyth, and its true local host is as yet unknown. Cattle grazing about the hill have been examined without result and the specimens were obtained by one of my students, Mr Kenrick Evans, who sent a white terrier through the bushes and subsequently searched its coat. By this means specimens were taken in November 1913, and January, February, and March 1914. I also obtained one crawling upon clothing in July 1915, near Llanfihangel y creuddyn.

I obtained several specimens of this tick, under very similar conditions, near Kingsbridge, Devon, during the hot summer of 1911, but I have never succeeded in finding it upon farm stock.

I am indebted to Prof. Nuttall and Mr C. Warburton for the identification of a number of specimens.

Red Water (*Bovine Piroplasmosis*).

"Red Water" is one of the chief troubles of the N. Cardiganshire farmer, and there is no doubt that in most cases the cause is tick-borne bovine piroplasmosis.

I have received sixty complaints and in almost all I ascertained that the tick *Ixodes ricinus* was present, frequently in large numbers.

Prof. G. H. F. Nuttall has reminded me that "red water" may be due to toxic plants, but I am unable to say what plants may be responsible for the trouble within the area surveyed, although it is everywhere firmly believed that the disease is due to cattle eating alder (*Gwern*) and oak leaves, and farmers insist that outbreaks follow the grazing of cattle on or near woodlands or rough swampy places where alders are abundant. It is in just such places however, that *I. ricinus* is most common. The rough ferny pastures, rocky hillsides and wooded valleys and slopes frequently swarm with this tick, and several farmers state that at times the cattle come home so covered with them that they can be scraped off, while poultry will pick them off the cattle while standing and lying about the yards. Fern cutters are often troubled by the ticks and I have come across several cases of sores resulting from their careless removal from the flesh. I have extracted a number of the hexapod larvae from my own limbs after passing through fern, etc., and in September 1915 I captured dozens of these larvae crawling upon my hands and arms after handling some dead bracken. I have also frequently collected this tick from dogs, cats, sheep, etc. in all parts of the area, and it is interesting to note that no case has yet been reported to me from the upland pastures and peat lands. It will be seen that the affected land includes much of the rough peaty soil of the Dyfi Flats, and the wooded valleys. I have known cases due to cattle being turned into the woods to graze during May and June, because it was too early to send them to the hills, and the lower fields had been closed for hay.

Severe losses have occurred on a number of the infected farms, sometimes during the spring and early summer, at other times in late summer and early autumn; the majority of outbreaks being in May—June and again in August—September. Several cases have come under my notice in which red water farms have changed hands, with the result that the new occupier has soon had to deal with a more or less violent outbreak generally resulting in severe losses, in one instance ten cases and three deaths.

After several troublesome seasons the disease abates in both the number of cattle attacked and the virulence of the cases, and it is probable that this is largely due to the acquisition of a degree of immunity by the herd, and the occurrence of mild cases among the stock when young: some local men have noted these mild cases among their calves. On many farms the disease is quiescent just as long as the herd remains self-contained, and only calves bred upon the place are reared; but should cattle be bought from non-immune stock the trouble speedily reappears, often within six weeks of purchase, and this is very generally recognised; stores bought in October become ill in the following May. I have heard of several cases of "red water," in calves that had never been allowed out, and hence must have contracted the trouble from the litter, which is often dried fern or other rough herbage.

A "slope" farm (600 feet) had considerable trouble with piroplasmosis while the neighbouring holdings remained free. After a time however the disease appeared upon the adjoining farm below, after the cattle of both holdings had grazed adjoining fields and had probably been in contact. The year prior to the commencement of the survey, a third farm adjoining the second became similarly affected.

A farm on the Dyfi Flats formerly greatly troubled with piroplasmosis where also ticks are very abundant, has latterly been much affected by salt floods owing to some sluice defects, and the cattle have been forced to drink much brackish water. The owner claims that trouble from the disease has now practically ceased, although ticks are still abundant.

Certain rough fields, in different parts of the Area, that were known to cause red water in cattle grazing them, have been rendered harmless by a process of improvement consisting of clearing away rough growth and the application of basic slag. One man claimed to have lost twenty-three cattle in two years. A farmer in the extreme north of the Area who had been troubled with red water, was advised by Sir S. Stockman to graze sheep with his cattle and this proved successful. Neglect of the precaution for two years resulted in a return of the trouble.

Several farmers state that they never had a case of piroplasmosis until after purchasing an animal, or lot of cattle from certain places: these all proved, on enquiry, to be "red water" farms. The disease is locally known as "*pisso gwaed*" = bloody urine, and in severe cases "*dwr ddu*," or black water. Local remedies vary from a quart of brine and 1 lb. of Epsom salts, and other mixtures including ginger, cayenne, spices, etc., to "the ashes of an old boot sole" administered as a drench.

Good farming, and the adoption of reasonable precautions should go far towards the elimination and avoidance of the dangerous diseases classed as red water whether tick-borne piroplasmosis or due to a plant (or plants) as yet unrecognised.

Psoroptes communis, var *ovis*.

Sheep Scab, once the bane of the local sheep industry, is now well under control as the result of compulsory dipping. It is doubtful whether this pest is now really endemic within the Area surveyed, most of the cases that occur being imported during the autumn movements.

Sarcoptes mutans.

Scaly leg of fowls. Only observed once or twice.

Blood-Sucking Flies.

Although aware that certain species were at times very abundant in the Survey Area, I identified only a few prior to the summer of 1916, when special attention was given to the group.

The hay season was particularly hot and dry (following a wet time) and all classes of farm stock suffered severely, the working horses in particular, and I several times observed as many as five species about the same horse.

The Home Farm, Crosswood, was used for special observation though others were visited. Local farmers and labourers agreed that never before had so many biting flies been seen. Coastal farms certainly suffer less than those inland and near woods.

I. *Ceratopogon* sps. One or more species of this genus are a serious plague in many parts of the Area. I was severely attacked in the Llyfnant Valley and about Glandyfi in the extreme north of the Area during the evenings in July 1915: about Llanrhystyd Road, three miles south-east of Aberystwyth, as early as April 18th, in 1914, and at Crosswood (in the south) during July and August 1916. Specimens from this latter locality were carefully examined and did not agree with either of the species figured by Austen[1], but was near *pulicarius*. Probably several species are present.

II. *Simulium variegatum* Meigen. I obtained nine specimens from the nose and jaws of a mare at Crosswood on July 20th, 1916, and about

[1] *British Bloodsucking Flies.*

ten days later a number were taken sucking blood from the belly of a working horse, in the same locality. Some of the flies were engorged with blood.

III. *S. ornatum* Meigen. One specimen, Crosswood, early August, from the belly of a working mare.

I am indebted to Mr F. W. Edwards[1] for this identification and also for verifying that of *S. variegatum*. Both species were taken in the evening and none were observed during the heat of the day although searched for.

IV. *Haematopota pluvialis* Linn. This is an exceedingly abundant form after mid-June, and in the lowland country is a great pest to working horses. On June 28th, 1914, on the wooded bank of the Ystwyth I counted between thirty and forty upon the back of a man wearing a dark coat, and at Crosswood on June 21st, 1915, I killed 200 upon four working horses in a few minutes.

In 1916 they were present in great numbers, especially during the hot dry weather of July and early August. Rain and cool winds at once mitigate this pest. Many were examined but none of the other species of the genus were detected. The earliest date for the species in my notes is June 8th, 1915, near Talybont, one specimen in the grip of an Asilid fly; I was bitten at Crosswood on the 10th, and saw the fly in abundance at Llanfarian, near Aberystwyth on the 12th.

V. *Therioplectes distinguendus* Verrall. This beautiful species was common at Crosswood and also near Aberystwyth, attacking horses during July and early August 1916. At first I took it to be *T. solititialis*, but the characters agree with Verrall's *distinguendus*.

In every case the abdomen was "very extensively bright brownish orange, even to the fourth segment[2]," though there is a considerable amount of variation in the black dorsal central line. The belly and legs of the horses were invariably the parts attacked. The flight is silent, and the ♀ is easy to capture once she has settled. Cattle are also attacked.

VI. *Atylotus fulvus* Meigen. I obtained two females while they were sucking blood from horses at Crosswood during July 1916, and one similarly on August 1st. I also observed but failed to capture three others. This handsome fly possesses a rapid and silent flight, and is by no means easy to obtain being very readily alarmed.

[1] Edwards, F. W. "British Species of Simulium," *Bull. Ent. Research*, Vol. VI. June 1915.

[2] *British Flies*, Vol. V, p. 371 et seq.

VII. *Tabanus sudeticus* Zeller. After examining a very considerable series of females and comparing them minutely with Verrall's descriptions of both *T. bovinus* and *T. sudeticus,* I consider the local specimens to be referable to the latter species. I also obtained one male, resting on *Calluna* at an elevation of 800 feet near Pontrhydgroes, September 2nd, 1916, which is undoubtedly *sudeticus.*

All authors however admit that these two species are difficult to identify, and Verrall[1] (p. 392) says "Even the very large species *T. bovinus* has been separated into two species which have been confounded for more than eighty years, and in this work I have recorded specimens which do not clearly answer to either of these two." This Tabanus is abundant in the Area, and ranges widely. During the summer of 1916 it was particularly plentiful and attacked all farm stock indiscriminately causing great annoyance, more especially among working horses, which were driven frantic and rendered difficult to control. The smaller species were as nothing compared with this great fly.

Their abundance may be judged when I say that I could easily fill a killing bottle in half-an-hour from a pair of horses during the hay harvest (at Crosswood) and a waggoner killed between twenty and thirty on one horse during a morning's horse hoeing.

I noted three sucking a newly-born calf and three upon one pig, while I was able to grab three with one stroke of the hand, from a cart mare.

The flight is most powerful, and the deep hum produced terrifies cattle. I was interested to observe a Hereford calf of six weeks old which was attacked while out in the open. This young animal did not rush to its mother near by, but instantly galloped to a small open stream about 100 yards away and stood in that facing upstream, and I did not again see the calf molested while standing in the water. It is interesting to note that with horses the lower fore legs and feet are the parts most frequently attacked, but sometimes the back is also selected. In cattle, the sides and belly are attacked, whilst in sheep the middle of the back is almost invariably chosen, and the same applies to pigs.

I have seen a few settle upon the legs of men working in the field. Cattle, although greatly irritated, seem to be bitten but seldom, a free use of horns and tail keeping the fly from settling long enough to bite; I observed a cow, with her tongue, kill a specimen of *T. distinguendus* that had settled under the brisket.

I have sat among a herd of cattle sheltering under the shade of a

[1] Verrall, op. cit. p. 392.

large oak and noted how averse is *Tabanus* to enter the shade; any cow venturing forth would be instantly assailed, while those on the outskirts would be hurriedly visited and again left.

VIII. *Tabanus cordiger* Wiederman. I found this species to be fairly abundant at Crosswood in July and early August, 1916. I only saw it attack horses, and chiefly the legs and belly.

The flight is silent, and in habit this species is much slower than the others so far mentioned; Verrall (p. 413) records this species from Barmouth, on the authority of Col. Yerbury.

IX. *Chrysops quadrata* Mefgin.

X. *C. caecutiens* Linn. Although a sharp look out was kept during the progress of the Survey, not a single specimen of the genus *Chrysops* was seen until the hot dry weather of July 1916, when a limited number of the above two species were obtained.

Two females of *C. quadrata* were taken from the head and neck of a working horse in a hay-field at Crosswood on July 20th, and similarly two of *caecutiens* on the 28th on a shire mare at Rhos Cellan, near Borth. Next day, two females were taken from a shire at Crosswood, while one of each species were collected on July 31st. In these cases the head and neck were chosen for attack.

A specimen of *Chrysops* was noted upon a Kerry sheep on July 30th, but not secured.

WARBLE FLIES (*HYPODERMA* sps.).

Whilst visiting the farms of the Survey Area in 1913—14, and again in 1914—15, constant attempts were made to obtain information regarding these cattle pests. The data gathered, however, did not prove to be satisfactory for several reasons, first, the larvae are not obtainable throughout the year, and farms visited during some periods naturally did not yield results; again unless the cattle were either in the buildings or readily available personal observations were difficult, and the obtaining of specimens practically impossible; lastly, the local farmer although generally able to say whether his cattle were subject to attack or not, could give no help as to which species was present, and not infrequently overlooked the pest altogether.

I therefore decided to make a special series of visits during the spring of 1916, to farms throughout the Area at varying altitudes and in different situations, in order to gain some definite information on the subject. In all twenty-five farms were visited and about 170 cattle examined. Samples of larvae were thus obtained from sea level to

1500 feet, and from the coastal pastures to sixteen miles inland. The farms were taken in groups in the various divisions of the Area between February 23rd and May 22nd. In February the larvae were immature and by the latter date many had left the cattle.

H. bovis was obtained from only three herds, in all others *H. lineata* was the species present, and there is no doubt that this latter is the abundant form for the whole Area.

Of the few cases in which *H. bovis* occurred, one was near Devils Bridge, ten miles inland and some 800 feet above sea level. Another was a coast farm from which young cattle are annually sent to another holding ten miles away and seven inland, for summer grazing. *H. bovis* occurs in both these holdings and has probably been carried from one to the other, but which may be the original situation I am unable to say.

In the third case the larvae were immature and I am not absolutely certain as to the identification. Regarding *H. lineata* then as the usual local species, I do not find any district free from the pest; it occurs alike from sea level to the highest sheep walks (where a few cattle are generally kept) and I have found it abundantly in cattle grazed throughout the season about 1000 to 1500 feet. The species appears to be very prevalent around the Dyfi Flats, but everywhere some herds are more heavily infested than others. Young cattle are certainly more severely attacked than others, and it is interesting to note that calves kept indoors until September and then turned out proved heavily infested in the following spring. I have examined young cattle of ten months old in which the whole back was one mass of lumps, forty to fifty have been counted on heifers and young cows, but old cows, in my experience, seldom show more than a dozen and frequently very few, or none. I further incline to believe that black cattle suffer more than do those of lighter hue, the worst infected herds and individuals that I examined were all black.

Very little is done in the Survey Area to combat this pest, but several farmers claim great reduction or almost entire absence owing to dressing their cattle with a carbolic wash, such as a sponge dipped in McDougall's or Jeyes' Fluids, and applied from time to time.

Only two of the herds examined proved totally free and of these, one is carefully dressed with carbolic, while the other, a small dairy farm, has to my knowledge not shown a warble for three years, although the next farm is lightly affected. I attribute this freedom to the fact that throughout the season these cattle graze the damp shady fields near a river.

The only local name I have met with is *cynron gwartheg* = cattle grubs or maggots; this being used on the hills and sheep walks. Although not common, warbles are by no means rare upon horses, and a number have been reported; only one larva however reached me and that in but poor condition; this larva greatly resembled that of *H. lineata* but was smaller and is probably *H. equi*.

Gastrophilus equi Fab.

The Horse Bot Fly is fairly abundant. I have seen them ovipositing upon horses from July to September. In the early part of that month in 1916, I observed this insect ovipositing upon a pony mare and foal at 1000 feet elevation. The foal when approached by the fly, at once lay down and rolled.

The ova can be seen in abundance upon working horses, and bots have been sent me from horses that have died from various causes.

Melophagus ovinus Linn.

There is no doubt that the greater frequency of dipping now practised helps considerably to control this sheep pest, but it is still abundant and large numbers of adults and pupae may be obtained at most mountain shearings. Several complaints as to its excessive abundance were made to me. In well-cared for flocks, especially in the lowlands these insects are not common; they are known locally as *llau defaid*, or sheep lice.

Lyperosia irritans Linn.

I have been bitten by this fly on several occasions but have never found it in any numbers.

Sheep Maggot Fly (*Lucilia sericata*).

This is undoubtedly one of the most troublesome pests of the Area and is the cause of considerable loss. The trouble is always particularly severe during bursts of heat following showers, and should such a period coincide with hay or corn harvest a combination of circumstances likely to produce the worst results will have arisen. Everyone is then fully occupied and the sheep are frequently less carefully tended than usual. Sheep when attacked at all badly, usually hide among herbage, etc., and since such herbage is then very abundant and the correct precaution of counting the sheep and looking up any that may

be missing is often omitted or slurred during busy times, it is not surprising that some are overlooked and either die undiscovered, or get into such a state that treatment is difficult, and sheep so injured are long in recovering. Many farmers lose from one to four sheep annually from this cause.

The wooded valleys are, as might be expected, the worst affected, and maggots are there an annual occurrence, though in degree in accordance with weather conditions. Many farms have a wide vertical range and may include:

1. Riverside meadow varying from good grass to rank gorse and rushes.

2. Wooded slopes, with fields interpersed.

3. Open upland which may either be bare, or more or less heavily covered with fern and gorse.

The higher and barer the grazing area, the less liable are the sheep to attack, but the presence or absence of fern and gorse are most important factors for several reasons:

(*a*) Sheep that graze among fern are liable to become wetted and to remain wet longer than those grazing in the open, and damp sheep are more liable to attack than dry ones. Damp sheep, especially if untrimmed and at all dirty, give off a strong odour which doubtless attracts the fly. Shepherds say that sheep grazing among fern are especially liable to attack about the head, neck and shoulders, as these parts are wetted by being pushed among the fern, which, together with the grass that generally grows in its shelter, retains dew and rain water long after the barer portions of the land have dried.

(*b*) Sheep attacked in such situations have a much greater chance of avoiding detection, unless very carefully hunted up.

(*c*) The flies doubtless find shelter among rough vegetation.

Fern and gorse, or a combination of these, but more particularly deep fern, extend the danger zone for maggot attack for a great distance upwards. A ferny mountain means trouble with maggots. There are summers, cold, wet, or windy, during which maggots are practically unknown on the higher sheep walks, and but little is seen of them even in the wooded valleys and lowlands. There may be a short period during which attacks occur, and the period may be of considerable duration, or a series of outbreaks may occur. All depends upon atmospheric and climatic conditions, which may be strongly modified by the presence of woodland, gorse or fern, etc., and by the attention of the farmer and shepherd.

During the very worst periods it seems that isolated cases occur about even the very highest parts of the Area.

An old sheep farmer of great experience put it thus: "They (the maggot flies) go up and down the mountain (Plynlymon) just like the thermometer," a better simile would be hard to find, since it is the rise and fall of temperature that governs the activities of the flies.

It was quite usual during the late summer and autumn of 1914, to observe a considerable proportion of ewes and lambs in the lowland fields with either "broken fleeces" or with patches sewn on to the wool.

Shepherds state that sheep that have been travelled or hard driven, and so heated, are very liable to attack, the fly being probably attracted by strong odour. I have examined a number of the farms that complained of severe outbreaks and made enquiries and observations on others that were unusually free and elicited a good deal of information particularly with regard to dipping. This is a vexed question and is locally the subject of perennial and vigorous discussion; the whole matter is affected by sheep scab and compulsory dipping times. For dipping purposes Cardiganshire has been divided into two areas, a northern and a southern; the line between the two starts from the centre of Aberystwyth and follows the main road to Pont Erwyd; thence it is continued up the river Rheidol to the county boundary. North and west of this line it is compulsory to dip between September 1st and November 15th, and south of it between July 15th and August 31st. These dates are arranged to combat sheep scab and on account of them, earlier dipping against maggots is often not undertaken. Some farmers wait until the compulsory period before dipping at all meanwhile merely treating "struck" sheep with solutions of dip from a bottle; these men have usually the greatest trouble and losses. Others adopt the protective method of dipping before the compulsory time, but still too late; and only comparatively few dip about the commencement of the danger period; these few, even when in a bad district seldom have serious cause for complaint especially if careful supervision is exercised between dippings. There are a few farmers who dip as often as three or four times, commencing in June, but the average time appears to be July, and late in the month rather than early. The idea of dipping against maggots seems to have been obscured in this Area by the trouble with sheep scab, which pest has now, fortunately, been controlled.

Several makes of dip are in use in the Area, and having regard to the often irregular and unsatisfactory manner of use it is difficult to criticise their relative values. All kill maggots satisfactorily, but there

is no doubt that some afford a much longer period of protection against recurrence of attack than others. Some dips are obviously better suited for use in summer, others for winter, and too wide a use is made of carbolic dips during the summer without the addition of sulphur. There appears to be room on the market for both types of dip if their correct values and limitations are recognised. A sulphur dip was formally in use locally, consisting of 1 lb. of powdered sulphur to 10 gals. of water, and is said to have been very successful as an anti-fly remedy. Certain mountain and hill districts which are so situated as to be especially wind swept, seem remarkably free from maggot. Long tongues of hill land flanked by deep valleys and swept from end to end by the prevailing west to east winds seem most favourably influenced, and bare connecting ridges and spurs of similar aspect likewise. Anything in the nature of shelter whether due to a depression, or lee side of vegetation, etc., has a prejudicial effect. Sunny aspect has an effect also, especially in conjunction with the above features.

The salt marshes, otherwise so healthy, are by no means immune from the pest; although open and treeless they are frequently thickly covered with rushes. I have also had bad reports from the sandy coastal margin.

Odd cases may occur as early as April (I once saw a bad case in the last days of March on the S. Pembrokeshire cliffs after an exceptionally hot spell) but trouble seldom becomes serious until June and usually not until July: by mid-September danger may be considered over.

The following are typical reports obtained from farmers and shepherds and refer to a period of years unless a particular year is given.

I. A sheep walk with about 1500 sheep present during summer time; elevation 900—1400 feet.

No maggots before June, then according to weather conditions. One or two cases daily in ordinary fine weather, but if conditions favourable one to two dozen cases might occur for several days, more especially on the lower part of the hill which overlooks a valley, lies in the sun, and where there is more fern.

(I have attempted an estimate of cases for such a place, as follows:

Period of liability:	June	30	days,
	July	31	,,
	Aug.	31	,,
	Sept.	15	,,
	Total	107	or say 100 days,

allowing

	40	days without cases		
	40	,, with 1 case daily	=	40
	10—12	,, ,, 5 ,, ,,	=	50—60
	8—10	,, ,, 10 ,, ,,	=	80—100
Say	100	days with a total of		170—200 cases.

1500 or 1600 sheep and 160 cases would enable us to estimate say 10 % for the season. Many of these would be slight and the fleece unbroken.)

On lowland farms the percentage might be 20 % or higher.

II. Farm part bog and salting, and partly pasture along the margin of wooded slopes; 200—300 acres, about 200 ewes kept. Maggots very troublesome especially on the bog land.

III. One of the most experienced shepherds speaking of the flanks of Plynlymon states that several years may elapse during which very few cases will occur, then comes an especially hot time with showers followed by an outbreak involving the whole area.

Larvae of *L. sericata* obtained near Talybont on June 1st, 1915, from a ewe that had just died from their attack, hatched June 27th—29th. Very severe attacks took place during suitable weather July 1st—7th, 1914, and June 1st—9th, 1915.

Sheep maggots are known locally as *Cynron*.

Blue bottles (*Calliphora erythrocephala* Meigen) undoubtedly cause some trouble, but the chief loss is due to *L. sericata*.

SHEEP NASAL FLY (*Oestrus ovis*).

Considerable difficulty was experienced in obtaining accurate information regarding this sheep pest. Enquiries made at the commencement of the work informed me that losses had occurred within the Area about the years 1900—1904. I subsequently made extensive enquiries, and after obtaining data from thirty-five sheep farmers and shepherds, have arrived at the following facts. A severe outbreak commenced in the summer of 1900 resulting in heavy losses during the spring and early summer of 1901. Trouble and losses continued during 1902—3, and apparently the disease waned and practically ended in 1904. The outbreak was of a very sudden nature and most of my informants stated that this trouble had not been seen before or since. Sheep men in the south of the Area declare that the trouble had come

to them over the hills from Radnorshire; while others, in the north, make similar allegations regarding Merioneth. There is always a marked tendency to blame other districts or farms for troubles that have very probably originated at home; and some people carried this to the length of blaming some English rams that had been used in the Area, as the source of trouble.

It is my opinion that the disease is at all times endemic to a greater or lesser extent, but what factors govern its sudden increase I am unable to say; investigation at the period of an outbreak would probably yield the required information. From statements made by several of the older men, it is evident that another very similar outbreak occurred in 1884, or thereabouts. It is by no means easy to obtain the correct dates for past occurrences, among a people who seldom keep any records. All agree that this outbreak was "some years ago"; others are fairly certain that it was "ten or fifteen years ago." Fortunately one farmer had entered and dated his losses and kept the old books; while the local veterinary surgeons were able to help me to some extent.

Losses ranged from one or two up to fifty or sixty per flock during 1901—2. One owner had sixty ewes affected out of a flock of 200, but by standing them in pens in which quick lime had been spread, and by constantly repeating this process, many larvae appear to have been sneezed out and no losses occurred. The whole of the uplands appear to have been involved, though in varying degree.

The general health of the flock and the state of the individual is considered to have played an important part in relation to losses (as is usual with parasitic diseases). Flocks kept in good condition suffered much less than those in a poor state, while more ewes died than wethers, the former being weakened by lambing and suckling. One or two men claim to have noted slight cases since 1904. I have myself observed sheep behaving in a suspicious manner, placing their noses to the ground, etc., and I instituted further enquiries in 1915, this time among butchers' assistants and slaughter-house men. As a result, I obtained, during May, two infected heads, one from the south of the Area, and another from a few miles beyond the southern boundary; while in April 1916 a third was sent from S. Cardiganshire. In each case the number of larvae present was small. It is therefore evident that the fly is normally present in small numbers, but, as is the case with other insects, liable to become suddenly abundant.

How far the purchase of infected sheep may tend to spread this pest by importing it into fresh districts remains to be proved. A farm which

possesses a wide vertical range, noted cases in February 1901 among sheep pastured on the lower levels (250 ft.), while those kept upon the hill (1000 ft.) did not show pronounced symptoms until May. A remedy largely tried during the outbreak consisted in either pouring a few drops of turpentine, or a teaspoonful of turpentine and linseed up the nostrils, one nostril at a time.

Trichodectes sphaerocephalus.

Sheep lice are abundant at times among the mountain flocks, and are known as *llau cochion bach* or little red lice. Shepherds state that they are worse after wet weather, or a wet winter, and upon sheep weakened by any adverse conditions.

This pest also is largely kept in check by the dipping regulations.

LIVER ROT OF SHEEP, AND BIONOMICS OF *LIMNAEA TRUNCATULA* IN THE ABERYSTWYTH AREA.

By Chas. L. WALTON, M.Sc. (Wales).

(*Departments of Zoology and Agriculture, University College of Wales, Aberystwyth.*)

(With 5 Text-figures.)

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I. General Notes on the Area.

Introduction.

In the autumn of 1913 I was instructed to commence a Survey of the Agricultural Zoology of the Aberystwyth Area, and in particular to study the Liver Rot of Sheep and the bionomics of *Limnaea truncatula*

the host snail. The work in 1913–14 was of a preliminary character and the grant from the Board of Agriculture and Fisheries was renewed and increased for 1914–15 and again renewed for 1915–16.

It speedily became evident that no hard and fast boundary line could be adopted, and while particular attention was given to the Area as defined for the other Surveys (Geological, Botanical, Economic, etc.) yet I did not hesitate to go further afield in order to gain a more comprehensive view of the problems, and to obtain additional data. In fact, had this not been done, one of the districts most affected by Liver Rot, and, at the same time most typical of much of Mid Wales would have been overlooked, since it commences at the very margin of the original sheet selected for investigation: Ordnance Survey 163 (small sheet series). Further, several groups of farms were examined well outside the Area to act as "controls" and for purposes of contrast. Such groups were examined at (*a*) Kerry, Montgomeryshire; (*b*) Llandrindod Wells, Radnorshire, and again a few about Llanddewibrefi and neighbourhood somewhat to the South of the Survey Area, in South Cardiganshire.

Topography of the Aberystwyth Area.

The Area surveyed comprised North Cardiganshire and some adjacent borders of Montgomeryshire, and may be roughly defined as O. S. sheet 69 (large sheet series) excluding the portion of Merionethshire in the N.W. and, roughly, an eight mile wide strip of country running N. and S. to the extreme E. of the sheet; though the Area also included a few farms lying to the south of the sheet. Roughly the boundaries are:

To the W. and N.W. (coast and river)	22	miles
,, North	8	,,
,, East	18	,,
,, South	16	,,

say 250 square miles.

The surface Geology of this area may be broadly described as follows in three main divisions—

I. The mountainous upland tract of solid rocks frequently covered by a considerable depth of peat. The rock succession is only irregularly exposed in deep stream cuttings, while these valleys are occupied by boulder clay and river deposits.

II. The coastal plateau consists of rock and boulder clay. The clay is usually exposed and rarely covered with peat.

III. The fall line, which is intermediate. Here the boulder clay generally follows the valleys, and is usually covered with a thin layer of peat. Much of this is readily cut through by small streams.

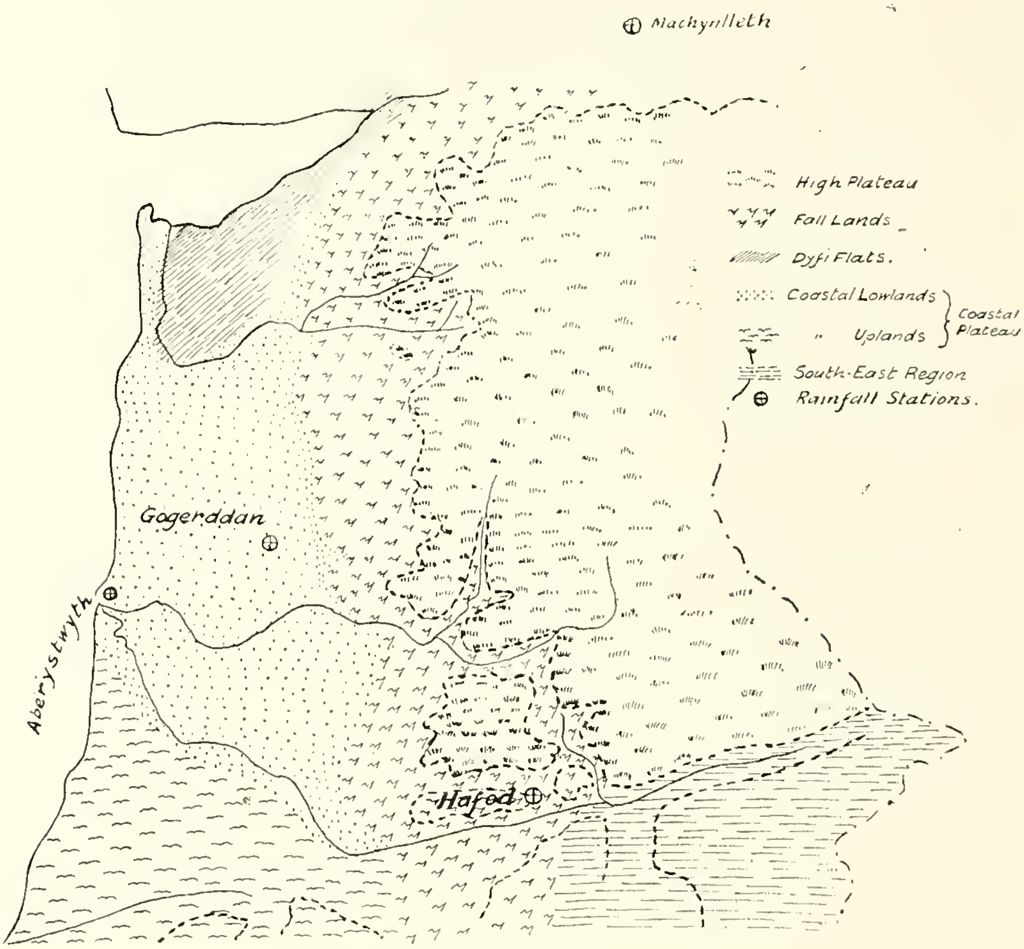

Fig. 1. Map of the Aberystwyth Area, Wales.

The Dyfi Flats form a distinct type consisting largely of peat but with a few well defined tracts of tenacious clay (alluvium).

Two areas are of special significance, namely, Devils Bridge, Rhos-y-gell; and South of Ysppytty Ystwyth as far as Pontrhydfendigaid. These large districts are floored entirely by boulder clay and are ill drained.

Near the western edge the plateau rises from a longitudinal (N. and S.) valley occupied by sections or tributaries of the Rheidol, Ystwyth and Teify to a small watershed, running from North to South. This has the feeders of the longitudinal valley on its Eastern side and the torrent streams of the plateau edge on its Western.

The watershed is pierced in several places by plateau edge streams which have "cut back," but in the North, where the longitudinal valley is slight, and the large area of high plateau rises quickly to Plynlymon, there is, along the watershed, a series of lakes between 900 and 1400 feet above sea. Most of these have been utilised and altered in connection with the formerly very extensive lead mining operations, while "leets" conducting water from these lakes mark the hillsides in all directions as also do the remains of the numerous spoil heaps and ruins of former mine buildings. The deleterious effects of these lead workings upon stock, crops and fisheries within the Area is being dealt with by others, and will merely be mentioned here as a distinctly adverse factor on the general Biology of the Area. This High Plateau is the great summer grazing area for sheep. The fall line or slope between this High Plateau and the lower Coastal Plateau is of considerable extent and importance and includes much of the woodlands of the Area; the land is frequently rough and ill drained, and the numerous streams often occupy deep ravines or cwms. The Coastal Plateau is almost entirely composed of the "Aberystwyth Grits" of Silurian age, and contains the best cultivated agricultural land within the Area; here also, naturally, is grouped the bulk of the population.

The only town within the Survey Area is Aberystwyth, and the main mass of the population lies in its vicinity, although there is a considerable chain of villages lying along the main road from Aberystwyth to Machynlleth, namely Bow Street, Llanfihangel, Talybont (a large village), Taliesin, Tre'r'ddol, Eglwysfach, etc.

The chief rivers are as follows: to the N.W. the Area is bounded for some distance by the estuarine portion of the River Dyfi, and flowing into this portion are several streams which, rising on the mountains, flow westward through steep rocky valleys until they reach the Dyfi Flats, whence, seaward, they now largely occupy artificial channels, considerably affected by tidal flow. The chief of these from N. to S. are, the streams that join and then occupy the Llyfnant valley; the Einion, Clettwr and Leri: this latter being longer than the rest and receiving a number of tributaries from the Cwm Ceulan, Cwm Ty-nant, etc.

Several streams following a similar course to the above unite and empty into the sea at Claraeh Bay $1\frac{1}{2}$ miles N. of Aberystwyth. The two chief rivers of the Area however, are the Rheidol and Ystwyth. The first mentioned is formed from the streams Camdwr, Llechwedd-mawr, Hyddgen, Hengwm, etc., upon the slopes of Plynlymon and the adjacent mountains, and after taking a southern course for some eight miles turns westward at the Devils Bridge. The Ystwyth rises among the mountains south of Plynlymon, and, like the Rheidol, reaches the sea at Aberystwyth harbour after a eourse somewhat similar and parallel to that river. In the extreme S.E. of the area the watershed of the Teify is reached and, southward the gorge of the Wyre Stream, practically forms its boundary.

The rainfall of the Area is considerable and varies greatly in the different districts. It will be considered in eonnection with the bionomics of *L. truncatula*. From the point of view of the Agricultural Zoologist the Area surveyed is divisible into six chief divisions each with its own typical pests and diseases.

Natural Divisions of the Area.

These are approximately outlined in Map I, and are as follows:

(*a*) The great central mountain mass of the High Plateau, chiefly natural sheep pasture; very lightly populated and with a heavy rainfall.

The typical troubles of this region are Gid in sheep and cattle and Fox damage to lambs.

(*b*) The Fall Line or Fridd, typified by rough hillsides and ravines, often wooded, the ehief diseases are Bovine Piroplasmosis; Sheep Maggot; Liver Rot; Pigeon damage, Warbles, etc. (This passes in turn from N. to S. into the following.)

(*c*) The Dyfi Flats, also known as Y Gors Fochno, or Borth Bog; a flat largely undrained area of peat, salt marsh and alluvial pasture with here and there rocky eminences or "Islands" (Ynys). The region is bordered on the N.W. by the river Dyfi, on the W. by sand dune and storm beach, and on the E. by the last mentioned Fridd (here heavily wooded) and to the S. by the next type. The chief complaints are Bovine Piroplasmosis, Liver Rot, Sheep Maggot and Fox damage.

(*d*) Coastal Lowlands: a eomparatively highly cultivated farming area, lying chiefly around Aberystwyth, and bounded on the N. by the Dyfi Flats, on the E. by the Fridd, Westward by the sea and to the S. passing into the next type (*e*). The bulk of the dairy farming of the

area is carried on in this district, and many lambs are "wintered." Principal troubles, Husk, Warbles, damage by Fox (to fowls) and by Rooks (to crops), Rabbits, Wireworms and Flea Beetles, but it is seldom that any of these are very severe.

(*e*) This is a continuation of (*d*) but reaching higher elevations; it may be called the "Coastal Uplands." It is roughly a triangular region occupying the s.w. corner of the Area. A well marked ridge of high land occupies the coast and the remainder is hilly farming land, in places rough, in others good. Several streams occupy deeply cut, steep sided valleys. The rainfall is not particularly heavy (though official data are unfortunately lacking) and dry slopes, are the chief feature: Wireworm, Flea Beetle, and Rooks are the principal causes of complaint.

(*f*) An ill defined region coming in to the s.e. of the Surveyed Area is known to myself as the "Wet Clayey Mountains." It comprises an expanse of bare, ill drained high land with heavy rainfall. The wooded valley of the Ystwyth cuts through the n. and n.w. portion. It abuts upon (*a*) to the n. and n.e. and is separated from (*e*) by the Fridd (*b*). The Agriculture is poor and the chief disease Liver Rot.

Methods of Work.

The work of the Survey has been carried out as follows: October, 1913, to September, 1914. An enquiry was at once instituted to determine the occurrence of Liver Rot and the distribution of *L. truncatula*, and a number of typical farms were visited in order to gain a close knowledge of local methods of Agriculture, more especially sheep farming.

During 1914–15 the greater number of farms throughout the Area were visited and enquiries made regarding the Agricultural Zoological pests, and histories of these.

The study of the distribution of *L. truncatula* was continued and very numerous observations were made from time to time at a number of field "Stations" and experiments conducted in the Laboratory in order to study the life history of the mollusc.

In the final year, 1915–16, the visiting of farms was concluded and much time given to observations and experiments with *L. truncatula*. The distribution of Warbles and the species of Biting Flies, etc., were also given particular attention. Maps were prepared and the Report drafted.

Throughout the whole Survey, first place has always been given

to field work, in fact, so much time was taken up by visiting farms, etc., that little consecutive laboratory work was possible. The Area surveyed is a wide one and in parts rough and inaccessible. It was necessary to visit series of farms at different times of the year, and mountain farmers were often hard to find; this involved a return to many places. In addition spots inhabited by *L. truncatula* had to be visited regularly in all parts of the Area. The weather in the mountains was frequently very adverse and much arduous walking had to be undertaken, other methods of transport being negligible and train services by no means convenient during the winter.

Many of the local agriculturists have been most helpful, and have given all the information and assistance in their power, only a small minority being either uninterested, or unwilling to give information or facilities for investigation.

My sincere thanks are due to Prof. C. Bryner Jones, M.Sc., Prof. H. J. Fleure, D.Sc., Prof. O. T. Jones, D.Sc., Messrs W. E. Whitehouse, M.Sc., F. S. Wright, J. Pryse Howell, E. Morgan, M.R.C.V.S., D.V.H., J. J. Griffith, B.Sc., R. G. Stapledon, M.A., F. W. Flattely, T. A. Stephenson, and many others for kind assistance and advice. I am greatly indebted to Miss Thomas of Aberystwyth for permission to use local Meteorological data collected by Dr A. Thomas; also to the British Rainfall Association and the Meteorological Observers at Machynlleth and Gogerddan.

I also tender my thanks to numerous friends throughout the Area surveyed for much help and hospitality.

II. Liver Rot.

Distomum hepaticum *in the Area.*

This Trematode flat worm is the cause of perpetual trouble to a number of sheep farmers within the Area and has in past years caused very severe losses among the flocks. The last outbreak was waning when the Agricultural Survey commenced in the autumn of 1913.

The life history of this parasite is now so well known, and has been so often described that it is not necessary to recapitulate the details here. During the progress of my work particular attention was given to the life history and bionomics of the intermediate host, the mollusc *Limnaea truncatula* without which the worm cannot complete its life cycle. Consequently its distribution is entirely dependent upon the distribution of the snail, and the factors governing the latter have been

carefully studied (the results will be found under *L. truncatula*). The last outbreak of liver rot was by no means so widely distributed, nor was as much havoc wrought as was the case in some previous epidemics. Nevertheless, a number of flocks were decimated, and considerable loss occasioned among the others, particularly in the Dyfi Flats and S.E. regions.

It would seem that both host and parasite are naturally able to maintain themselves permanently within the Area in favourable situations, which, given suitable conditions, serve as centres from which they may spread.

A considerable number of livers infected with *D. hepaticum* came into my hands, and it was once reported to me from cattle, although I failed to obtain any of the specimens, which were stated to have been very large.

It is probable that in certain regions the majority of the sheep harbour a few of these parasites, which however, are seldom present in sufficient numbers to cause serious disturbance. Drafts from these flocks sold each autumn distribute the ova of the flukes over a large area thus tend to perpetuate the cause of future trouble.

I have nothing to add to previous descriptions of the parasite or the disease; but in connection with what has been said above, I may add that although ewes may suffer from flukes for several years and even finally find their way to the slaughter house as "fat," yet the livers of many are found to be atrophied and hardened to the consistency of leather.

I do not know of any local name for the fluke other than the general term *pryfed*, a worm, the disease, however, in addition to the word rot, is known by several terms, and of these *pwd* is the most general, and really refers to the dropsical swelling that frequently appears beneath the lower jaw consequent upon the lowered position of the head while grazing. *Pwdri* (rotten) is often applied to the condition, and the word "rot" finds its equivalent in *wedi rotio.* To the North of the Area the word *pock* is used for liver rot.

Methods of Combating the Liver Fluke.

The presence of the disease has a considerable effect in modifying the systems of sheep farming, various methods being adopted to mitigate and prevent its appearance, the following being the most usual:

1. A few farms possessing wet clay soils capable of giving severe general infection have given up keeping sheep.

2. Sheep are kept away from suspected fields or places. An interesting variant which only came to my notice a few times, is that sheep are only allowed upon ground known to be otherwise dangerous either during, or after, sharp frost, a good example of the result of careful observation by intelligent men, who will generally find some way out of difficulties which prove too great for others. Many farms are able to safeguard their flocks to a large extent by keeping them on dry land during the most dangerous periods, and the practice of "summering" lowland flocks upon the mountains (dry grass or peat) results in a great reduction in the numbers exposed to infection.

   There is no doubt, that, taken as a whole, a kind of rough adjustment has taken place (chiefly the result of actual trouble) which in normal time prevents heavy losses.

   One farmer will maintain a successful flock where another would lose it, largely a matter of individual observation and knowledge, as is no doubt also the case with some other endemic diseases. Speaking generally, rot occurs in this Area in many instances through accident, unforeseen circumstances, or carelessness.
3. The farmer changes his system; ewes are bought in afresh each autumn and sold again after producing one crop of lambs. It is noted that ewes that have been on the same farm for several seasons will suffer from the cumulative effects of flukes.
4. Sheep are only bought to graze and fatten, and hence are only on the land for a limited period, or "tack" sheep are taken for the winter months only, when the chances of infection are generally greatly reduced.
5. Experienced and astute men examine the eyes of sheep before purchase and may thus detect cases in the earlier stages. Sheep on infected farms are similarly examined from time to time, and suspected sheep "culled" to curtail further loss. Certain farms that make a practice of selling sheep each autumn, to lowland flocks, are troubled with endemic rot, and buyers, in consequence, may suffer losses. Such farms in course of time acquire a bad name and may have some difficulty in disposing of their stock, these people, not unnaturally, are chary of giving information as to the presence of the disease among their flocks, and may deny all knowledge of it. This aspect of the case somewhat hindered the work at times, and had to be met by other methods,

and it was generally possible to obtain infected snails from such land. There exists a practice, I am informed, of placing infected sheep on good pasture, etc., to be "flushed" prior to their being offered for sale, as this greatly assists in "clearing" the eyes, at any rate temporarily.

6. Some farmers, and owners, have eliminated the disease from their land by drainage, and on many places this can be effected with comparatively little trouble and expense, whereas on others, it would prove to be a task of great difficulty.
7. The shepherd in charge is frequently able to prevent, or at least mitigate the losses from rot to a considerable extent, and many, without being aware of the true cause, yet know that rot follows grazing on wet land. They may even go further, and suspect, or actually accuse, some definite spot, and either endeavour to prevent sheep grazing there, or will "cull" those that make a habit of feeding on that particular ground. It is well known that certain sheep will develop a taste for the herbage of wet spots (often locally called "wells") and remain there persistently, and they are in consequence especially liable to contract the disease. One old shepherd likened this habit to "taking to drink." It will be observed that the precautions listed vary with the degree of infection, whether slight, partial, considerable, or severe.
8. It is the custom, on some farms that suffer from rot, to turn their sheep, or give them access to a dry bank by night, and it is claimed that this procedure greatly mitigates the trouble. It is simply allowing or following out the movement naturally performed by sheep when conditions allow them sufficient freedom. Seventy three distinct localities inhabited by *Limnaea truncatula* were discovered within the Area during the progress of the Survey, and after comparing my map of these spots with his map of the surface Geology, Prof. O. T. Jones finds that practically the whole are situated upon clay.

   The correlation between the presence of clay, *L. truncatula* and rot is therefore very marked.
9. During my enquiries I met several farmers in whose flocks a case of rot may occur now and again, and who then promptly kill the sheep as soon as they detect the symptoms, believing that such is a preventive measure. There is no doubt that such action may be very wise, one owner tracing all his trouble to the

purchase of an infected ram, and it is possible that this animal introduced the disease upon the farm. Another farmer makes a practice of grazing colts with sheep in a wet field, known to cause trouble; the colts are believed to eat the dangerous herbage without being affected thereby.

In Montgomeryshire "Blue grass" (*Luzula* sp.) is blamed as a cause of rot, while in Radnor worm casts, locally called "worm spews" are regarded as the origin of the disease.

10. Close grazing is considered by observant farmers and shepherds to be one of the factors conducive to attacks of rot, and is of course linked with over stocking. Many sheep in competition will eat what would otherwise be avoided. Infected snails frequently live on mud below thick vegetation, or water containing cercariae may flow over portions of a field causing a growth of rank grasses which only become dangerous to sheep when eaten down.

 There is a very general idea throughout the Area that the application of lime to grass land is often followed by an outbreak of rot, while one farmer from outside the Area made the same statement regarding Basic Slag. Sometimes the statement was merely general, but I obtained more or less definite details in seven instances. In all cases the ground treated was wet (ill drained) grass land with clay (or peat and clay) soil. The explanation seems to me to be that the application of lime, etc., to the land results in an improvement and "sweetening" of the herbage, with a consequent increase in the intensity of grazing by the sheep, thus finally reaching the lower grass upon which cercariae have become encysted.

It is evident that condition, as usual, plays its part; on some farms and indeed, in some districts, the presence of some flukes may be regarded as usual, and those flocks, that have become reduced in condition through overstocking, poor pasture, bad weather, exposed situation, etc., may suffer as severely from a moderate degree of infection, as a strong flock when much more severely parasitised. It is also notable that rot and lead poisoning are often to be found at the same time and farmers and shepherds state their belief that sheep grazed near lead mines are very liable to rot. It is largely I believe a case of reduced vitality enabling the flukes present to produce a greater effect.

The presence of the dropsical swelling or "bag" (*cwd*, Welsh) under

the jaw is locally considered the chief external sign of the disease though some of the more experienced men recognise that a sheep may show this symptom and yet recover, or may be attacked and not show it at all. It is, however, generally regarded as denoting a severe case, though I have seen an ewe that showed this symptom in February and yet reared her lamb successfully. A number of ewes will pull through until lambing time and then die, as I have myself witnessed. The usual local treatment for rot, consists of slitting open this "bag" with a knife and then rubbing in salt. This may be done several times and is claimed as a cure, and instances are cited where sheep have recovered after the treatment; from what has been said it will be evident that recovery might result without the operation. One ewe is stated to have been "cut" three times and later reared three lambs ere being sent to the butcher three years later, her liver was then found to be "like a stone." Occasionally a seton is put in the "bag."

III. OBSERVATIONS ON THE BIONOMICS OF *LIMNAEA TRUNCATULA*.

The Distribution of L. truncatula *and* L. peregra.

Upon receiving instructions to study the Liver Rot of Sheep and the Bionomics of *L. truncatula* within the Aberystwyth Area, in the autumn of 1913, my first endeavour was to discover as far as possible the distribution of the disease through the Area, and at the same time to trace the occurrence of the host snail. I speedily discovered that two species of the genus *Limnaea* were abundant in the Area: *L. truncatula* and *L. peregra.* One solitary specimen of *L. palustris* was found in Feb. 1916, in a streamlet at the head of the Teifi watershed on the extreme southern margin of the area examined.

It also became apparent that *L. truncatula* and *L. peregra* showed a marked difference in habitat. Although frequently found in the same stream or ditch, their distribution is but rarely found to coincide, and when this does occur, it is in the nature of an overlap, one species or other predominating.

The bionomics of *L. peregra* were followed to some extent also in order better to understand *L. truncatula.* In general the life histories and distribution are similar; in detail they differ. The main physical features of the Survey Area have already been outlined; it will therefore suffice to say that the chief factor governing the distribution of the species is the distribution of clay; in this Area frequently of glacial

origin; rock, gravel, sand and peat are, in general, devoid of these mollusca.

Since *L. truncatula* is very widely distributed (even occurring on the islands of the w. coast of Ireland) it may be taken that its antiquity is considerable and it may have followed the retreating glaciers of the ice sheet; its habitat would be governed by whatever modified the distribution of clay and it would readily extend its upward range by crawling slowly upstream, while floods would, in some cases, renew its downward distribution. Given suitable conditions both species occur throughout the Area from sea level to 1250 feet, and there is no doubt they would range higher were conditions right. Speaking broadly, *L. truncatula* inhabits shallow streams and ditches with a clayey floor, or layer of diatomaceous mud; *L. peregra* prefers a deeper mud and a less rapid flow. Where these conditions merge the two species may overlap to a limited extent.

In one or two deep ditches *L. truncatula* was found to inhabit the margins and sides (sometimes crawling on the damp zone just above water level) while *L. peregra* occupied the softer and deeper mud about the centre. This ditch ran east and west, and there were decidedly more specimens of *L. truncatula* on the eastern side, than on the more sunny western, and more crawling above the water line. Peat—one of the most important physical factors of the Area—is inimical; at any rate I have failed to find *L. truncatula* among peat, while in water draining from it the size is small and the shell thin.

It is probable that peat acids, lack of lime and the presence of much soft flocculent vegetable matter are the limiting factors, and not any lack of food. It sometimes happens that clay is exposed around the margins of peaty tracts, and there *L. truncatula* will often be found, thus causing dangerous spots in an otherwise free area. The following may be cited as an example: in November, 1913, I examined a small holding situated in the S.E. region, and about 800 feet above sea level. This place is just on the boundary of a large expanse of boulder clay, and so many sheep had died from rot from time to time that the occupier despaired of keeping any. After examining several boggy ditches without result, *L. truncatula* was at last discovered in a muddy patch just where drainage from a little lane entered the fields. On tracing this drainage to its source it was seen to ooze out of a wet patch on the margin of an otherwise dry grass field, this spring marking the margin of the boulder clay.

The streamlet was next followed downward, and clay showed in its

bank for a considerable distance, but the vegetation became more and more peaty. The streamlet follows a bank and hedge which bend somewhat, and thus receives the majority of the drainage from the ill drained peaty field above; consequently the lower portion receives more drainage than the upper and finally the clay is hidden under peat. Below the bend, I was unable to find *L. truncatula.*

I was for a long time puzzled to account for the absence of *Limnaea* from peat and several factors were studied successively, namely:

(1) Peat acids,

(2) Food,

(3) The relative size of the foot of the mollusc.

That peat acids play a part is beyond doubt since *Limnaea* from the vicinity of peat, or within the influence of peat drainage are usually stunted and small. Buddicom[1] says of *L. truncatula* at Church Stretton "Lime is necessary for the construction of the shell, and among land forms on the Longmynd I have found small fragile forms of *Vitrea*, while specimens of *L. truncatula* in springs on the hill side are much distorted, with thin transparent shells."

Taylor[2] also states "Granitic soils, peaty districts, or other formation deficient of the calcic carbonate of which shells are mainly composed, are characterised by shells not only of thin texture but dwarf size." I cannot say that I have found any *Limnaea* from the Aberystwyth Area to be either deformed or dwarfed, merely smaller than the normal and thin shelled. I now consider the chief factor governing the difference in distribution of *L. truncatula* and *L. peregra* (and their absence from peat) to be the relative size and expanse of foot.

In *L. truncatula* the foot is small and the shell a narrow spire, while in *L. peregra* it is relatively much broader as also is the shell. *L. peregra* is able to travel upon the surface of soft mud in which *truncatula* would sink, as is readily observable during the progress of field and laboratory work. It is significant that the newly hatched young of *peregra* are almost invariably to be found crawling upon the water plants or stones on which it is hatched, while *truncatula* when young is more often to be found in similar situations than during later life.

L. truncatula will leave a soft substratum for a harder if food be there available, as for instance fallen leaves that have become coated with a

[1] Buddicom, R. A. (1900), *The Land and Fresh Water Mollusca of Church Stretton*, pp. 182–195.

[2] Taylor, J. W. (1895), *Monograph of the Land and Fresh Water Mollusca of the British Isles*, Pt. II, p. 85.

deposit of diatomaceous mud; it dislikes the soft mud upon which *peregra* dwells and will crawl away from it, if possible.

Food of L. truncatula *and* L. peregra.

In order to ascertain the food of *L. truncatula* the intestinal contents were carefully examined at different times of the year, and were found to contain mud, consisting for the most part of quartz fragments, etc., together with residual vegetal matter. The mud amidst which the snail lives and feeds consists of the same particles of inorganic matter as were found in the intestines, together with the remains of decayed vegetation a number of Diatoms and occasional Desmids.

Prof. Fleure considers that the radula form in this mollusc is well fitted for shovelling in this mud.

L. peregra shows very similar intestinal contents, the only difference being that the organic particles are much finer, but *peregra* as already stated, prefers mud of softer and finer texture than does *truncatula.* It has been stated that grit is retained in order to act as a "grinder" but if the excreta of *L. truncatula* are examined microscopically they will be seen to consist largely of quartz fragments similar to those found in the gut. Entire frustules of Diatoms, have also been detected in the excreta and it is my opinion that the mud is ingested in order to obtain the Diatoms. Snails were washed clear of all mud and placed in tubes containing water only, and their excreta, as long as any were passed gave the same result.

Forty samples of mud were collected from all over the Area and examined microscopically. Some were from streams and ditches devoid of either species of *Limnaea,* others were from spots inhabited by only one species, some were from clay, others from peat.

In practically every case where *L. truncatula* was found Diatoms were common or abundant, and a few Desmids were present; where *peregra* only occurred no Desmids were recorded, but Diatoms were fairly common, but where neither were to be found Diatoms were small and few in number and species. Diatoms are abundant in peaty streams, etc.

L. truncatula continues to feed throughout the year and growth is of course more or less continuous also, (in this Area and during the course of the Survey at any rate) snails collected during Dec. and January at 1000 feet above sea level and at water temperatures as low as 38° F. showed the same intestinal and excretory content and activity as those collected at other times.

L. truncatula placed upon mud containing much organic matter, and taken from a pond not inhabited by these mollusca, left this mud persistently and climbed the sides of the dish. If placed on a sod from a stream margin and supplied with clear water from their own stream they crawl out, or up the grass stems and these fix themselves and die of drought; but should diatomaceous mud be added, they will remain upon it and live for considerable periods, sometimes for months, provided a suitable supply of food and water is maintained[1].

Growth rates vary considerably, but, although continuous, are certainly slower in winter than during the more favourable months. In the majority of cases it is evident that *L. truncatula* hatched in the autumn does not reach a length of 5 mm. until the following Feb. or March, while those hatched in spring make very rapid growth and attain 5 mm. in eight or nine weeks.

Movements and Migrations.

Mention has been made already of a ditch in which *L. truncatula* occupied the sides, the centre being too soft for that species. *L. peregra* was very abundant in a stream and pond not far away and in March, 1914, this stream dried and I removed 80 specimens to the ditch in order to prove if possible that *L. peregra* would live under the conditions which I regarded as favourable to it. This batch was placed in one spot in order to watch any migration that might take place. On April 28th, another 50 were added from the pond, making 130 in all. By May 1st, many had disappeared, possibly owing to the depredations of water rats, since signs of these animals were numerous about the spot. The ditch became very low during the summer and by Oct. 23rd, some of the snails had spread down stream for a short distance. Just after this the ditch was cleaned out prior to the commencement of the autumn rains and on Jan. 28th, 1915, only one very large specimen could be found out of the original 130, while *truncatula* had completely disappeared. By Feb., 1916, *L. peregra* had become abundant and occupied 40 feet of ditch below the original point of colonisation, but upstream they had extended as far as conditions were suitable, being then arrested by a sharp increase of slope which caused the bed at that point to be scoured clear of mud. I have always found that *peregra* will advance against a current at a surprisingly rapid rate, averaging in one instance two yards per day. I have never noted any such habit in the case of *truncatula*.

[1] If placed upon soft *L. peregra* mud, *L. truncatula* crawl out if they can.

L. truncatula will readily float upon the surface film in quiet water, and I have frequently observed this to take place under natural conditions, and no doubt the snail may at times be thus transported down stream for short distances.

Growth rates have already been mentioned and as temperature largely governs this some notes were made from time to time at varying dates and elevations and it may be of interest to give a selection here. The shallow streams inhabited by *L. truncatula* are evidently rapidly affected by the air temperature and thus by temporary climate conditions. In all the examples given below *truncatula* was present in abundance.

Effects of Temperature.

1. Near Ysbytty Ystwyth, 700 ft. Dec. 1st, 1913, Air 56° F., Water 49° F.
2. Near Ysbytty Ystwyth, 800 ft. Dec. 10th, 1914, Air 42° F., Water 41° F. *Note.* White frost morning and evening, Cercariae given off by snails.
3. Near Ysbytty Ystwyth, 800 ft. Jan. 21st, 1915, Air 36° F., Water 38° F. Rediae in an advanced condition were present in snails.
4. Capel Bangor 120 ft. March 17th, 1916, Air 57° F., Water 53° F. A still warm day following white frost, sunny situation.
5. Glandyfi, 25 ft. (about) March 13th, 1915, Air 52° F., Water 49° F.
6. Near Ysbytty Ystwyth 700 ft. March, 1915, Air 39° F., Water 41° F. (swift), Water 40° F. slow flow.
7. Llanrhystyd Road 70 ft. (?) March 31st, 1915, Air 55° F., Water 51° F. A warm wet day, 4 p.m.
8. Near Ysbytty Ystwyth 900 ft. April 8th, 1914, Air and Water 47° F.
9. Near Ysbytty Ystwyth 1100 ft. April 8th, 1914, Air and Water 46° F.
10. Llanrhystyd 70 ft. (?) June 16th, 1914, Air 64° F., Water 59° F.
11. An interesting series of observations were taken on Feb. 24th, 1916, during a walk from Devils Bridge to Crosswood during a bitter east wind and snowstorm.

(*a*) Near Devils Bridge, 800 ft. noon, somewhat sheltered, Air 36° F., Water 37° F.

(*b*) Near Devils Bridge, 800 ft. 1.30 p.m., exposed to wind, Air 33° F., Water 34° F.

(*c*) Near Crosswood 250 ft. 3 p.m., sheltered streamlet, and under the lea of the mountains, 5 miles from (*b*), Air 36° F., Water 41° F.

During the very severe and prolonged frosts of the winter of 1916–17, attempts were made to procure specimens of *L. truncatula* from a ditch near Aberystwyth, but without success, notwithstanding the extreme severity of the weather, this ditch and a number of others, all shallow, and in exposed situations, contained *L. truncatula* in abundance, and of all sizes in March–April, 1917; while the deposition of ova commenced as usual during the latter month.

From this evidence one must conclude that frost can hardly be regarded as an adverse factor in the life history of this snail.

Oviposition.

Neither in the field nor in the Laboratory was *L. truncatula* ever observed in copula although carefully watched. Braun proved *L. auricularia* to be self-fertile and this may be true of other members of the genus. *L. peregra* on the contrary may be most readily observed to pair; the snails indeed (as has already been recorded for this species) being frequently seen to form chains of three or more. Jeffreys[1] states of *truncatula* "It deposits its spawn on the mud, and not like its congeners on the stalks and underneath the leaves of water plants." In my experience in this Area the ova masses are deposited either upon the mud, or on stones, leaves, twigs, etc. It is impossible to be dogmatic without having examined a very large number of cases, but it is my experience gained from a considerable number of examples, that one or other of these methods predominates, and it is largely governed by the condition of the spot inhabited. Should the flow of water be relatively swift and stones occur among the mud, ova will be deposited upon these, especially those that project above the mud, or, upon the top of such as may be level with the surface.

If the flow be slight and many leaves and twigs lie upon the mud these will be utilised (usually the under side of the leaf), but when the bottom is muddy, the flow slight, and fragments few, the ova are deposited upon it. Leaves may decay and fall to pieces after ova have been deposited upon them, thus leaving the ova masses free.

Each snail deposits several ova masses, there being from two to ten ova in each; seven to nine being the normal in my experience. Probably more are contained in the ova masses of the larger individuals (16 mm. in length is the largest specimen obtained in the Aberystwyth Area, but specimens over 10 mm. are exceptional) but I have chiefly dealt with smaller and younger snails, the majority of large adults being killed by summer droughts in 1915–16. The number of ova in a batch becomes less at the end of the period of oviposition when small lots of one to three ova are often deposited. The masses are irregularly rounded in form and are usually 3 to 5 mm. in diameter, and 2 to 3 mm. in height. They are clear and gelatinous, but generally become covered with particles of mud, diatoms, etc.

[1] *British Conchology*, Vol. I.

In the case of *L. peregra* the ova masses may be either rounded, oval, or sausage shaped, and contain up to 40 ova arranged roughly in either two or four rows (in the latter case two above and two below ::), and may measure 15 × 5 × 3 mm.

Ova were collected and hatched in the Laboratory and ova deposited in the Laboratory were also hatched, the time taken varying from four to six weeks. Ova that had been completely dried for periods up to 48 hours and then re-immersed hatched in the normal time; ova dried for longer periods were longer in hatching and the numbers surviving were greatly reduced, while in 1915 a few hatched from ova that had been dried for 100 hours. A number of Laboratory experiments failed owing to the ova being attacked by fungoid or bacterial parasites and careful and elaborate experiments begun under controlled conditions in ditches in the spring of 1916 with ova dried for 100 hours and over, failed, owing to unusual weather conditions which twice destroyed the apparatus.

Drought, and its effects upon the Snail.

Before discussing other points in the bionomics of *L. truncatula*, some statements of Prof. Thomas may be quoted, he says[1] "*Limnaeus truncatulus* is a fresh water snail with a brown spiral shell...it never reaches more than half an inch in length, while it is usually much smaller, a common variety in England, scarcely ever measuring so much as a quarter of an inch. Owing to its small size it often escapes notice.... Two or three kinds of snails most closely allied to *L. truncatula* (for instance *L. peregra*) may occasionally crawl out of the water for short distances, but in *L. truncatula* itself, the habit is so much more strongly developed that the snail should be termed amphibious. Indeed it is oftener out of the water than in it. When kept in an aquarium it quits the water and as often as it is put back insists on crawling out again, so long as strength remains. It is said to breed upon the mud on the banks of ditches." He then mentions that after eight days drought and then heavy rain, he found many dead snails, but others were capable of being revived; he continues "I collected a number of specimens and placed them in an open vessel on a shelf in a dry laboratory, in a position where the sun fell upon them for an hour or so daily. I found that rather more than half of them withstood 26 days of this treatment and some few recovered after more than six weeks. That

[1] *Journ. Roy. Agric. Soc.* 1883, pp. 292–3 et seq.

the snails can live on moist ground, quite away from any quantity of water for considerable periods, is sufficiently proved by the fact that I have kept them alive for eleven weeks on moist grass and moss, even when infested with the larval forms of the liver fluke."..."The snails thus left" (by floods) "continue to wander and feed, so long as the bottom of the grass remains moist. Even on land which is not liable to flood this snail may exist in large quantities, having crawled from the ditches, ponds, streams and marshy spots through the moist grass. A drought may render the snail dormant but, unless continued too long; it revives at the first shower of rain." In a footnote to another paper[1], Thomas quotes Sir C. Lyell who states that in Maderia, *L. truncatula* was accidentally introduced by the Portuguese, and spread so widely as to be found even in pools and ruts of roads. I have noted the snail in ruts on roads, etc., in the Aberystwyth Area, but have never observed any such phenomena of abundance after floods as in that noted by Thomas in Oxfordshire where conditions probably differ considerably from those found in Mid Wales. A considerable series of experiments were carried out to test the effects of drought upon *L. truncatula*. My experience during the last three years may be stated as follows: Direct observation in the field, and Laboratory experiments have both amply proved that the snail can resist drought for a relatively short time, though the time necessary to cause death depends upon both physical and meteorological factors which are very variable. Should the spot inhabited be a shallow hard bottomed ditch lying under a bank in full and continuous sun glare, the water evaporates rapidly and the death of the mollusc soon follows. Should the situation be a comparatively shady one, or overgrown, or floored with moisture-retaining mud, evaporation is correspondingly delayed and the molluscs have a greater chance of surviving a drought period. Many streams and wet spots are fed by springs and are not affected by a drought until it has lasted long enough to stop such sources of supply. Some spots are but rarely touched by drought, and there are a few in the Survey Area that have not dried since the work commenced; but these are very exceptional cases. *L. truncatula* never attempts to follow retreating water and when overtaken by drought remains with the mouth of the shell pressed closely to the ground. Thus even after a few days a comparatively damp spot may still remain under the shell, and should drought continue the snail withdraws further into the shell and so remains until either water returns or death supervenes. In damp

[1] *Quart. Journ. Microsc. Sci.*, 1883.

hollows, some proportion of the snail population of a ditch may survive, while the remainder perish, or only a few may die and the rest be saved by rain. Much depends not only upon situation, but also upon the water supply, type of soil, vegetation, duration of drought, amount of sunlight, cloud, fog, dew, etc., etc., rendering the whole matter complex.

Some snails will not recover when replaced in water after two days drying should they have been in a very exposed position and subject to continuous sun and dry wind; in other cases where more favourably situated from five to eight days may elapse. Should any of the snails however, become buried in the mud their chances of survival are greatly increased, and experiments conducted in May, 1916, in the case of snails buried beneath 2½ inches of damp soil, about half recovered when replaced in water at the end of 14 days, but after three weeks (artificial) drought all were dead. It has several times happened that one or two large snails will be found among the fresh stock of newly hatched young, following a drought and it is thought that these may owe their survival to burial. Perhaps the most frequent and probable cause of such burial is the trampling of certain ditches by cattle, this while crushing many, at times doubtless preserves a few.

Local Rainfall Data.

At the commencement of the Survey (Oct. 1913) *L. truncatula* was widely distributed in the Area and of considerable size. During the summer droughts of 1914–15 it was almost impossible to obtain a sufficient number of specimens to carry on experiments and observations. The spring and early summer of 1916 saw a great increase owing to wet conditions, but in July a drought again killed large numbers. It is well known that wet years are a necessary prelude to outbreaks of rot, hence examination of the local rainfall for a number of years should be of interest. The rainfall data obtainable for the Area are by no means as complete as could be desired. Full details are available for Aberystwyth (which however is not typical of those portions of the Area more especially troubled by Rot) and I have been able to obtain valuable particulars for Gogerddan (83 ft.) some three miles from Aberystwyth; Hafod (580 ft.) near Devils Bridge, and Machynlleth (41 feet) three miles to the N. of the Area (see Map, Fig. 1).

The Chart, Fig. 2, shows the relative amount of rainfall at these stations and the amount in inches between 1905 and 1915. Thus, within the Area surveyed the rainfall shows a difference of 15 to 25 inches between the coast and an elevation of 600 feet, 12 miles inland (Aberystwyth and

Hafod) while Machynlleth 41 feet, and nearer the sea, has a rainfall equalling Hafod. In the Plynlymon region the average fall may exceed 100 inches. It will be seen however from Table I that although they differ in volume there is yet a great similarity in the form of the graphs. It will further be noted that the years 1910, '12 and '13, were wet, that is, the period leading up to and including the attack of rot.

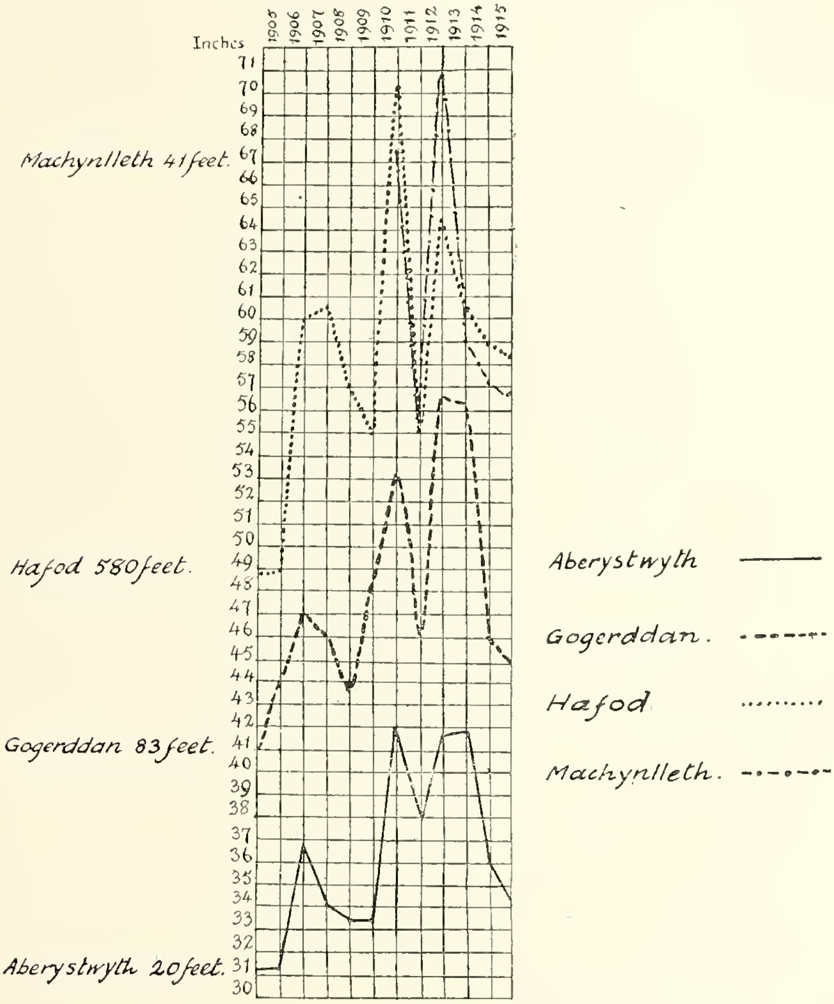

Fig. 2. Annual Rainfall—Aberystwyth Area, 1905–1915.

A very important point however, is the distribution of rainfall throughout the year and Table I gives the rainfall and number of days when rain fell at three of the local centres for 1910, '11 and '12, this shows that the number of raining days remains remarkably constant although the total amount of precipitation may vary considerably.

TABLE I. *Table showing Rainfall and Rainy Days.* 1910–1912.

	Aberystwyth			Gogerddan			Machynlleth		
	1910	1911	1912	1910	1911	1912	1910	1911	1912
Rain ...	42·18	37·54	41·70	54·51	46·45	56·75	66·54	55·65	70·71
Days ...	221	180	228	233	190	227	238	194	229

TABLE II. *Table showing Rainfall and Rainy Days. Aberystwyth,* 1905–1915.

Year	1905	1906	1907	1908	1909	1910	1911	1912	1913	1914	1915
Rainfall	31·37	36·88	35·46	33·56	33·65	42·18	37·54	41·70	41·97	36·12	34·65
Days	196	211	211	172	188	221	180	228	210	202	196

Table II illustrates the relation between amount of rainfall and number of raining days for Aberystwyth for the period 1905–15. It has already been shown how important a part drought plays in the bionomics of *L. truncatula* hence let us examine the records for evidence of marked droughts. Figs. 3–5 illustrate the monthly rainfall for Aberystwyth for the year 1908 (a dry year) and 1912 (a wet year) also 1915 a season that had a marked effect upon *L. truncatula* since almost all in the Area were killed.

In the charts (p. 255) the rainy days in each month are shown, and further the relation between days and inches per month. It must be borne in mind that relative evaporation plays an important part, and that a rainfall that would suffice in winter would not necessarily do so in summer, again, a monthly rainfall say in February or November of three inches distributed over 20 days would in all probability keep *L. truncatula* alive, whilst in August falling in thunderstorm showers of brief duration it would probably amount to a physiological drought sufficient to kill a considerable percentage.

Much, as I have said, depends upon the situation, but the factors involved are complex and each spot would need to be considered separately to gain a complete understanding. Still, a good deal can be learned from the charts given.

I have also made a close examination of the Aberystwyth rainfall data from 1901 to 1915 noting the number and length of dry spells of more than five days. The longest rainless spell was one of 23 days in September but, on the average, dry spells of more than 10 days are rare, and the dryest periods are usually those of light rainfall spread over a considerable period in summer. In July, 1911, for instance, only ·83 inches fell during that period, followed in August by 5·56 inches on 15

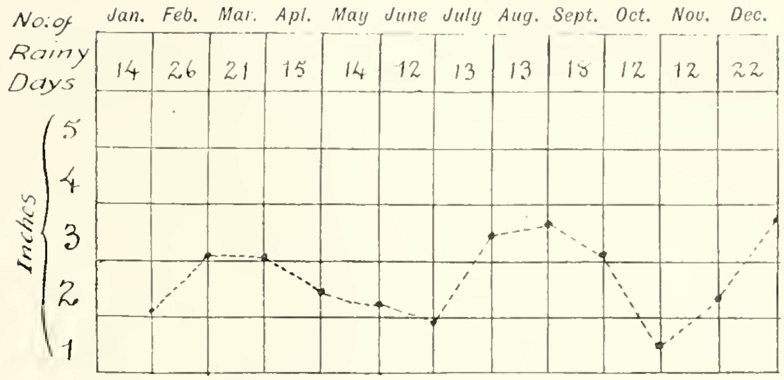

Fig. 3. Monthly Rainfall—Aberystwyth, 1908.

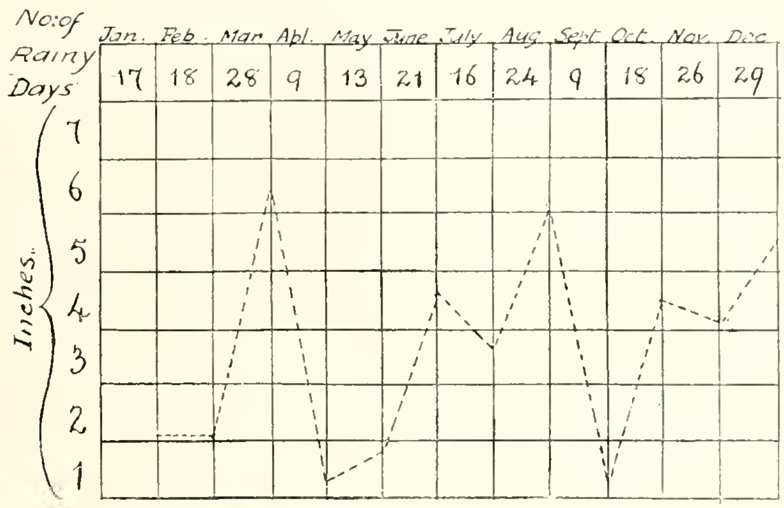

Fig. 4. Monthly Rainfall—Aberystwyth, 1912.

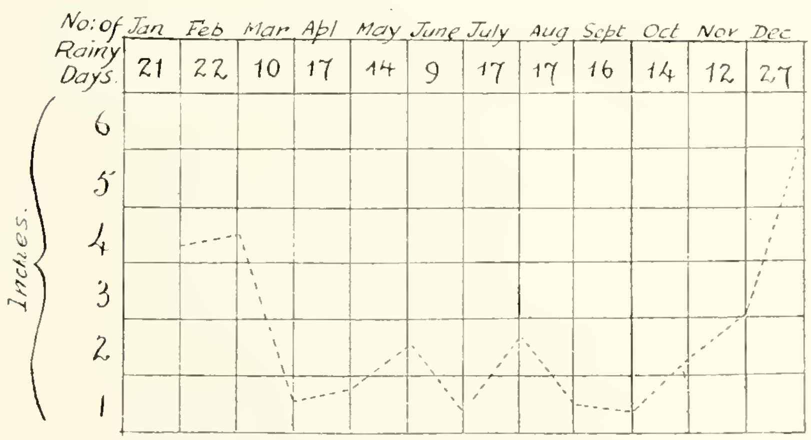

Fig. 5. Monthly Rainfall—Aberystwyth, 1915.

days with one straight dry spell of 10 days. In this Area all winters are sufficiently wet to allow *L. truncatula* to reach breeding size by spring, and it is wet summers that lead up to an outbreak of rot; while a drought in the spring will, in particular, assist in limiting its spread. One may say that the rainfall recorded for any particular year bears a very close relation to the number of rainy days. The number of rainy days, as has been stated, is fairly constant throughout the whole Area for any individual year, and it might be suggested that the Area is of such a character that droughts also are coincident. This means that no one district of the Area can act as a natural reservoir against paucity of *L. truncatula* in other districts, except in one district where suitable physical environment and a high rainfall coincide: there rot is endemic.

Sequence of Life History.

The general sequence of the life history of *L. truncatula* for 1915–16 was, as far as I could ascertain, as follows (all manner of variations of course occur, governed by environmental differences).

1915. November. Ditches refilled from direct rainfall or from springs recommencing to flow.
1915. December. Hatching of those ova surviving the drought period.
1916. January. " " " " " "
1916. February. " " " " " "
1916. March. All survivors of former generations and those of the new generations to attain 5 mm. in length (or thereabouts) commence to deposit ova.
1916. April. Deposition of ova continues as maturity is reached. Hatching of ova first deposited (after 6 weeks).
1916. May. Hatching continues.
1916. June (mid). First young snails of the year reach maturity and commence to deposit ova.
1916. July. Second generation of the year hatch (unless dried up).
1916. August. Dry, except in very favourable situations.
1916. September. Wet in early part, some ditches refilling.

Should drought not interfere, possibly a third generation would result, since ova deposited at the end of June should hatch by the end of July, become adult during September, and deposit ova in October. This sequence has not been observed since during each year of the Survey there have been prolonged droughts, and until 1916, the 2nd generation was only once noted (July 1915, without the Area). It should be possible, however, given suitable conditions, for three generations of snails to complete their growth in a year; allowing 17 weeks per generation.

Effects of Drought upon the Ova.

In no case of drying, natural or artificial, was *L. truncatula* ever seen to make any attempt either to burrow, to hide, or to follow the retreating waters, and was never found to have crawled voluntarily more than a few inches away from water. Prof. Thomas mentions a most important factor; namely grass. In my experience the presence of grass plays a great part not only in determining the period of survival of *L. truncatula*, but in governing largely the certainty and degree of recovery of the snail population upon the return of water after a drought. In other words grass acts as does a "mulch" in gardening practice in the preservation of moisture; and further, prevents to a large extent the removal of the surface layers of the ditch as dust by the wind, which otherwise takes place to a very considerable extent in exposed situations.

The ova masses, when dry, are hardly visible upon leaf or stone. The whole having shrunk to a hard scale much resembling a drop of dried varnish. No matter how long these have been dried (experimentally) in all cases I have found their original form to be resumed within a few hours following replacement in water.

Large numbers of snails of all ages and sizes were brought into the Laboratory from different localities and kept to observe at what size deposition of ova commenced. They were separated into lots allowing a difference of ·5 mm. in length between each lot, and from these experiments it is concluded that *L. truncatula* becomes adult when a length of 5 mm. is reached.

It was found impossible (owing to accidents, etc.) to prove experimentally that drying of ova masses causes a prolongation of the hatching date after the return of moisture, but very numerous field observations point to this conclusion. Ditches, etc., that became dry, and remained so, for as long as three months, all became re-stocked with *L. truncatula* during the following spring. This occurred both in 1915 and 1916. The dates of re-appearance of young snails vary considerably and it is my opinion, judging from many such cases, that the longer the desiccation the fewer will be their number.

The only spots that did not become re-populated in the spring of 1916 were a few that had been thoroughly cleaned out, thus of course removing all ova. Even some of those cleaned out (but not thoroughly) were subsequently found to be inhabited in the following year, sometimes to my great surprise. In every case care was taken to ascertain whether

or no such spots could possibly have been re-stocked from some pool or spring above, etc.

The exact date of hatching in such cases is often difficult to fix accurately, as the young when discovered only measure ·4 mm. to ·5 mm. in length and being often few in number and the ditch heavily grass grown, it is often almost impossible to detect them. These very young forms may crawl upon stones, etc. The whole matter is complex and would require very prolonged experiment to disentangle. The outstanding and important facts brought out by these observations are: that it is very difficult to get rid of *L. truncatula*, which will re-appear in ditches, etc., that have been completely dry for weeks and even months, and that apparently only thorough cleaning out, or a drought killing off all adults prior to the deposition of any ova, or ova about to hatch, will effectually clear any given spot. Conditions vary so much from place to place in the same locality that *L. truncatula* is not likely to be eliminated completely by natural means.

Obviously, should the ditches dry up before the deposition of ova the range of the species is seriously threatened, but once ova are deposited it would seem that the species stands a very excellent chance of survival no matter how hot or dry a time may follow, even if all the snails themselves are killed thereby. It may be urged that a wet period followed by a second drought would kill the hatching young and thus eliminate the snail from the locality and this is evidently a real danger, for in no case did snails appear from ova experimentally dried, when they were almost hatched. Newly deposited ova recovered after desiccation for certain periods. The difficulty however would be largely met by my hypothesis of delayed hatching consequent on length of desiccation. Again it may be pointed out that *L. truncatula* lives and deposits its ova in those portions of streams, etc., that are most liable to be affected by drought: namely the shallows and margins. Such situations are less liable to constant submergence, and even then, since some weeks must elapse before hatching can take place, it is obvious that only in a very wet year (or in permanently wet places) will hatching take place before autumn and this fits in with what I have observed.

How far these observations may tally with other areas, I do not know: different conditions may produce variations. It is however certain from my experience that ova masses just about to hatch will die if completely dried; while freshly deposited ova dried 34 to 36 hours hatch in about six weeks (the normal time). Ova dried for longer periods take longer to hatch and the numbers resulting are much

reduced but the data for this last statement are not so complete and are mainly obtained from field observations some details of which will now be given.

Field Observations upon the Life History.

While there is no doubt in my mind as to the facts deducible from the field observations, it has proved difficult to carry out the necessary controlled Laboratory check experiments when hatching is delayed for considerable periods, time, water and diseases of the ova being the chief troubles. As regards the first, much of my time was taken by field work, and duties as 2nd Lieut. with the University O.T.C. Finally, while controlled experiments attempted in a suitable stream near Aberystwyth on a small scale were fairly successful in 1915, an elaborate series arranged in the spring of 1916 were twice destroyed by most unusual floods.

The effects of meteorological and other conditions upon the life histories of *L. truncatula* and *L. peregra* will be best illustrated by following the sequence of events in one of the localities kept under more or less constant observation.

That about to be described is a streamlet situated some three miles from Aberystwyth, two from the coast, and flowing gently in a S.E. direction from the 100 feet contour line for a distance of some 200 yards down to a small muddy pool. This streamlet occupies a very shallow ditch at the foot of a bank, bordering the eastern side of a wide well kept farm road, and lies open to the sun. It is fed by springs rising in the sloping grass fields above, the sub-soil of which is glacial clay and detritus. The road is but little used for traffic, but a large herd of cows passes and re-passes constantly between farm and pasture, and these drink at the pool above mentioned and graze about and trample the ditch to a considerable extent. Sheep also are grazed in the fields from which the stream receives its supply of water and at the time of my first observation Liver Rot was present among them to some extent, not obtained from this ditch, but in all probability from the infected district from which they came (some 10 miles distant). It is also to be noted that rabbits are abundant near by, but I have no record of infected livers among them. Neither ducks nor fowls reach either pond or stream. The streamlet flows but slowly in its upper part and there contains a good deal of *Poa fluitans*, the slope being steeper, there follows a somewhat swifter portion and finally, near the pool, the flow is again slower and there is more mud. On March 27th, 1914, *truncatula* was of fair size and abundance in the upper portion, together with a

few *peregra*. Lower down *peregra* became more abundant and tended to occupy the centre of the stream while *truncatula* kept more to the sides, while near, and in the pond, upon the soft mud *peregra* was very abundant and *truncatula* totally absent. Newts swarmed in the pool. By the date mentioned the water had already become somewhat reduced and on the 31st, many specimens of *truncatula* were observed crawling upon the damp earth among the grass tufts bordering the stream and quite 18 inches from the water: the weather was showery. By April 28th this stream was dry, but in the damper hollows *peregra* was still alive. None were crawling but lay with the shell mouth pressed to the mud and the animal somewhat withdrawn. *L. truncatula* was scattered here and there chiefly along the grassy margins. Fifteen placed in water crawled almost immediately; the ground was not very dry, being sheltered by grass.

May 1st. The lower portion of the stream had been practically cleared of *peregra* probably by Moles which had furrowed up the mud in all directions. Higher up there were no signs of Moles, and shells were abundant, some already dead and empty.

May 3rd. A few *peregra* could still be revived in water, while of ten *truncatula* placed in a tube three proved to be quite dead, but the rest, although considerably withdrawn within their shells, soon expanded and in three hours the water swarmed with cercariae. From some of the emptied shells of *peregra* I obtained larvae, probably those of the beetle *Drilus flavescens* L.

Between May 3rd and 7th there was considerable rainfall and such molluscs as survived were crawling about as usual (by the latter date). I was then unable to re-visit this place until June 16th and by that date the stream was quite dry and not a single shell of either species could I find. From this date there was no rainfall sufficient to disturb the drought conditions. On Oct. 23rd the ditch was almost as hard as the road and covered with *Agrostis*, while the pond below had dried and had been cleaned out (the first time for years).

Both stream and pond were full of water on Jan. 28th, 1915, but no mollusca were discovered and another examination on March 18th yielded no better results, but by May 15th *truncatula* had appeared in the upper portion and a few *peregra* in the lower, and in June *truncatula* was heavily infected with *Distomum* larvae. The stream again dried and remained so until the middle of November; though a few *peregra* were still alive amongst mud in the pond below on Oct. 9th.

L. truncatula re-appeared by Feb. 1st, 1916, and were quite abundant

in the upper third although it had been roughly seraped out. During March *truncatula* beeame very scarce and the only eause for this that I eould diseover was the presenee in the fields adjoining of a floek of Lapwings, whieh are stated in the Leaflet, No. 44, of the Board of Agrieulture to feed upon this snail. A few survived however. During Mareh a eonsiderable number of *peregra* appeared in the pond, and by May 1st, several of these had erawled some ten yards up the streamlet. The weather eontinued wet and by June 14th *peregra* had reaehed the top of the streamlet; a progress of about two yards per day. During July the stream again dried up. Shelford[1] mentions some interesting faets regarding the upward migrations of some American mollusea from which he eoneluded that "there is no reason to assume that the migration began before the spring floods. If this is true the snails could make their way toward the headwaters at the rate of at least a mile per year if introduced into a large stream. This must be a response to both water pressure and eurrent. The opportunity to seeure sueh data is small."

Roadside Distribution and its Economic Effects.

A very large proportion of the loealities diseovered to be inhabited by *L. truncatula* within the Area examined are roadside ditehes and streams. Hundreds of likely plaees were examined in fields, upon hillsides, ete., ete., all over the Area, but it was eomparatively seldom that *L. truncatula* eould be found in sueh spots. Sueh plaees are frequently diffieult to observe owing to the amount of vegetation, and young forms might easily be overlooked; nevertheless I am eonvineed that the preponderanee of roadside loealities noted is genuine and due to their partieular suitability. I deeided to pay special attention to a series of these road sides, and some 50 sueh spots were visited regularly, and samples of snails examined for infeetion, growth rate, ete.

The reasons for seleeting these plaees were numerous:

1. They are more readily visited than many of the others.
2. They are for the most part distributed in groups in various parts of the Area and at different elevations.
3. They are subjeet in far greater degree to temperature ehanges, droughts, etc., and have thus served to bring out and illustrate many faets regarding infection, breeding habits, and bionomieal details.

[1] Shelford, V. E. (1913), *Animal Communities in Temperate America*, p. 106. Chicago University Press.

A considerable number of these spots had to be used in order to check results and gain mass of data.

4. These ditches are without doubt the cause of many of the sporadic cases of rot that are constantly turning up on otherwise free farms.

5. They are also responsible for more serious infection to sheep that stray from mountains and fields to graze by the road sides. Bad fences, gates, and walls (or their entire absence) contribute largely to this state of affairs. I know of several flocks that have been quite seriously affected through being allowed to graze by infected roadside ditches, while other neighbouring flocks not allowed to do so, escaped loss.

6. Infected water from these ditches is frequently allowed to flow over grass fields in a most dangerous manner. Almost every roadside ditch within the Area contains running water, and where conditions are suitable *L. truncatula* is to be found and very frequently heavily infected, and this infection is liable to be kept up from droppings of sheep either moved along the road or kept in adjacent fields. The water supplying these ditches is derived from:

(*a*) Direct rainfall.
(*b*) Springs arising in fields adjoining the road.
(*c*) Field drains.
(*d*) Seepage from ground on a higher level than the road.
(*e*) Ponds.
(*f*) Frequently a combination of these causes.

Where the slope is a long one (as is frequently the case in the Aberystwyth Area) the water is often led into a field in order to avoid flooding the road during heavy rainfall, and this may occur several times on a long hill or gradient. The water in each of these sections of ditch may have a separate origin and must be considered separately, and may or may not contain *L. truncatula*, which may or may not be infected.

Again, should even heavily infected water flowing into a field be conducted thence by a ditch which is kept open and reasonably free from vegetation, rot may be very rare or absent in sheep grazed there, because cercariae cannot become encysted upon the grass. The next field below, possibly belonging to another holding, may however become infected. The key seems to lie in a regular and systematic clearing out of ditches by those responsible, whether road authority, owner or tenant. Much land would be improved and loss in many cases avoided.

I have obtained strong evidence that the thorough cleaning of ditches completely destroys *L. truncatula* (at any rate for that season).

7. It is observable that these roadside snails are frequently infected with *Distomum* and this in successive generations, evidently the result of the passing and re-passing of the sheep, some of which are infected, thus supplying these ditches, etc., with a constant succession of ova.

Cercariae.

Hundreds of samples of snails were examined and cercariae obtained during every month of the year except August. In many cases they appeared in the water in the collecting tubes soon after the snails were obtained, often in large numbers. Samples were examined in order to ascertain the distribution of infection; and (as already mentioned) some ditches showed re-infection after the re-appearance of young snails.

Extensive experiments were conducted in order to gain some idea as to the relative number of cercariae given off by individual snails of various ages and sizes. In one series of experiments, specimens of *L. truncatula* were placed singly in glass tubes filled with clean water, and as soon as possible after collection. The water was renewed daily after counting the number of cercariae present. The results of a typical experiment is given in Table III. These experiments brought out several points:

(*a*) Cercariae were not given off by any snail of less than 4·5 mm. in length and are not abundant until a length of over 5 mm. is attained, and above that size they may be regarded as dangerous.

(*b*) As many as 70 cercariae have been naturally obtained from a specimen 7 mm. in length within 48 hours; while 40 to 50 were often obtained.

TABLE III. *Table showing the number of Cercariae obtained from ten specimens of* L. truncatula, *collected near Pontrhydygroes, Oct.* 22, 1914.

	Length of specimens in millimetres											
	3·5	4	5	5	5	6	6	6	8	8	Total	Average
Oct. 23	—	—	—	—	1	—	40	8	16	52	117	11·7
,, 24	—	—	—	—	—	—	40	5	1	7	53	5·3
,, 25	—	—	—	—	—	—	20	2	7	15	44	4·4
,, 26	—	—	—	—	×	—	×	3 ×	4 ×	25 ×	32	3·2
Totals	—	—	—	—	1	—	100	18	28	99	246	24·6

× = snail dead: remainder moribund.

(*c*) Those snails not giving off cercariae almost always outlived the specimens that were infected, which generally died.

(*d*) The majority of cercariae appear during the first day of an experiment and thence decrease in numbers.

This result may be due in some way to the waning vitality of the host.

Cercariae when extended and creeping by means of the ventral sucker usually measure 0·75 mm. in length (total). They swim with great vigour for a length of time varying (in my experience) with the vitality of their host; those from moribund snails either fall to the bottom, become encysted upon the walls of the vessel or lose their tails (and float in that condition) within 24 hours; while cercariae from active, healthy snails may continue to swim for some days. In one case some were still active on the 5th day after leaving the host. In all cases great care was taken that no fresh cercariae could have become mixed with those obtained each day.

While testing the vitality of *L. truncatula* dried both naturally and artificially, an interesting fact came to light. If infected snails that have been out of water for several days are re-placed in it, numbers of cercariae will frequently appear, almost at once, even should the snail be moribund. While experimenting to discover the food, etc., of *truncatula* a number of infected specimens were placed on a sod and immersed to the depth of an inch. Several of these crawled up stems of grass for about 1½ inches and there affixed themselves as usual under drought conditions. Two days later, wishing to test the effect of dew and rain shower upon such individuals I damped these until drops of water hung from or surrounded them. The snails did not move, but upon examining with a hand lens five minutes later the drops were seen to be full of active cercariae. The question arises then, would it be possible for a sheep to become infected directly by eating such a blade of grass, snail and all? It is also possible for animals to obtain from a pool or trough many living cercariae and others that float after having cast their tails. Despite repeated attempts I have never induced cercariae to encysts upon grass, they always settled and encysted upon the glass sides or bottom of the tube or dish.

An endeavour to ascertain the effects of cercariae upon the snails was made at my suggestion by Miss O. M. Rees, M.Sc., in 1915. Sections were cut of snails that had produced cercariae after capture and also of others not infected. The only conclusion arrived at was that, while difference were observable in the structure of the livers of the infected snails, yet no rediae or cercariae were recognisable.

On one occasion, in November, 1914, a sample of ten *L. truncatula* was obtained near Aberystwyth, and from two of these, in addition to the cercariae of *Distomum*, five of another species were noted, two from one snail, and three from another.

It was difficult to isolate these from among the others and an attempted sketch was not sufficiently good for publication. The chief points of difference were:

(*a*) The "tail" was much longer than in the cercaria of *Distomum hepaticum* (and the margin showed a crenate appearance), white in hue, and vigorously lashed.

(*b*) The body distinctly cordate when swimming and noticeably darker than the tail.

In April, 1914, cercariae indistinguishable from those of *D. hepaticum* were obtained from a sample of *L. peregra*: but although repeated attempts were made no further examples have been observed. These specimens were taken from a ditch containing numerous infected *truncatula*.

SUMMARY.

1. Certain flocks in the Aberystwyth Area having suffered considerably from Liver Rot, a Survey of the Agricultural Zoology was carried out between October, 1913, and October, 1916, special attention being given to the above disease and the bionomics of the host snail *L. truncatula*.

2. The Area comprised some 250 sq. miles of North Cardiganshire, etc., including Plynlymon, and falls into six natural divisions.

3. The presence of the disease has caused a number of local modifications in farm practice, designed to prevent, or mitigate losses. The disease was found to be on the wane within the Area, though endemic in certain places.

4. *L. truncatula* and *L. peregra* are the only abundant local species of the Genus. Considerable differences occur in the distribution of these two species. *L. peregra* was only studied in order to better understand the habits of *L. truncatula*. This latter species occurs in shallow water floored with Diatomaceous clayey mud, and is absent from soft mud, and peat. There is a marked coincidence between the distribution of clay and *L. truncatula*, and *L. truncatula* and Liver Rot.

5. The growth of the snails takes place throughout the year unless interrupted by drought or severe frost. Ova are deposited in March–April and hatch in May. The resulting snails, when they become

adults, measure about 5 mm. in length. They in turn deposit ova during June–July. Drought usually limits further progress until the late Autumn, the snail being often very scarce during August–September.

6. Desiccation speedily kills *L. truncatula*. Local environmental conditions—rainfall, aspect, soil, vegetation, etc.—play a very important part in respect to its survival. Rainfall and its distribution through the year is the most important factor governing the increase, spread, and infectivity of the snail.

7. The ova masses dry rapidly and then resemble a hard inconspicuous scale. They resume their former size and shape when moisture returns, and many appear to be able to hatch subsequently, though the amount of desiccation they will withstand is not yet determined. In spite of prolonged droughts, *L. truncatula* re-appears, unless ditches, etc., have been cleaned out.

8. Roadside ditches are very frequently inhabited by infected snails and the drainage from them may be the cause of cases of rot.

9. Cercariae of *D. hepaticum* were obtained from *L. truncatula* in large numbers practically throughout the year; but not from snails measuring less than 4·5 mm. in length. Seventy cercariae were given off naturally, within 48 hours, from one specimen measuring 7 mm. in length. Heavily parasitized snails are adversely affected. A few cercariae, resembling those of *D. hepaticum* were obtained once from *L. peregra*.

A CONTRIBUTION TO THE ANATOMY AND EMBRYOLOGY OF *CLADORCHIS (STICHORCHIS) SUBTRIQUETRUS* RUDOLPHI, 1814 (FISCHOEDER, 1901).

By FRED D. WEIDMAN, M.D.

(*From the Laboratory of Comparative Pathology of the Philadelphia Zoological Garden and the McManes Laboratory of Pathology, University of Pennsylvania, Philadelphia, Pa.*)

(With Plate V and 2 Text-figures.)

In 1814 Rudolphi described, under the name of *Amphistomum subtriquetrum*, a fluke from the caecum of the European beaver (*Castor fiber*). Little of importance was added for many years; i.e., until 1897, when Otto described it somewhat fully including its internal anatomy, and 1901 and 1903, when Fischoeder wrote of it in his classical revision of the Amphistomidae. In 1914 Duff described a similar parasite, this time from the American beaver (*Castor fiber canadensis*) which she believes to be identical with that of the European animal.

The present communication is offered in spite of the several preceding descriptions, first, because all of my material was immature and hence of some value from a developmental standpoint; second, because a wax reconstruction of the internal anatomy was made, allowing enlarged representation *in toto* with photographic accuracy; and thirdly, because previous descriptions could be collated with mine to give a fuller description than any yet published.

My material was obtained at autopsy from the caecum of *Castor fiber canadensis* dying on June 9, 1913, in the Philadelphia Zoological Garden with acute haemorrhagic enteritis (*P.Z.G.* 2936; *U.P. Path. Hist.* 4366). Although a careful search was made with the aid of a fine sieve, but eleven specimens were obtained, lying in the semifluid caecal contents, close to but not attached to the mucosa, which, contrary

to that of the small intestine, was in no way inflamed or otherwise pathologically altered. With them numerous oxyures were associated, of a species not yet determined.

The largest of the eleven specimens and a smaller were, while still moving, subjected to marked pressure between plate glass, fixed, and cleared in glycerin. The thickness of the worms thus treated permitted a determination of the grosser features only, with nothing of the minute and little of the grosser arrangement of the reproductive organs. A few ova were observed in the largest specimen which was teased with needles, the material being used in the succeeding determinations. The second, flattened specimen was cut serially in the frontal plane.

A third worm, which when entire measured 4·1 × 2·4 mm., was cut serially in the transverse plane. The specimens when fixed in 4 % formalin were not distorted or appreciably shrunken, but the third worm was reduced by the histological technique to 2·56 mm. in length, 2·2 mm. in greatest width and 2·0 mm. in greatest ventro-dorsal diameter as measured in sections. From the histological series drawings were made with the use of the Edinger projection apparatus, and from these a reconstruction of the internal anatomy was made by the wax plate method, omitting only the intricately formed structures such as vitellaria, nervous system and excretory ducts. All measurements hereafter given, unless otherwise noted, are taken from this third (shrunken) worm.

External Anatomy.

The specimens measure 5·1—6·3 mm. long × 3·0—3·5 mm. broad and 2·0—2·25 mm. dorso-ventrally. They are subcylindrical, the greatest diameter lying at the anterior borders of the acetabulum.

The posterior extremity is broadly rounded and moderately curved ventrally. The anterior extremity is more strongly directed ventrally so that the oral orifice points ventrally. The anterior extremity is broadly rounded and variably but never more than moderately attenuated, from which circumstance some specimens are pyriform and others subcylindrical. One specimen is exceptional; its anterior extremity tapers more than in any of the others and is recurved upon the body axis in the form of an inverted question mark. The margins of all are rounded and undefined; the dorsum is broadly convex, the caeca being often seen in fixed specimens with the naked eye and always with a hand-lens. The caeca appear as black bilateral areas posteriorly and dorsally and are sometimes traceable upwards to the

equator. The venter is flat transversely in its mesial portion, curved laterally, and strongly curved longitudinally. When fresh, the worms were pinkish grey and showed slight vermicular movement upon gentle warming; the movements were most marked in the anterior extremity and probably were responsible for the variations in the degree of attenuation noted in fixed specimens. When fixed in formalin they are of a grey green colour.

The oral orifice is terminal, directed ventrally, small, circular, unarmed, without papillae or other specializations, and measures 0·25 mm. in diameter. The genital pore lies 1·15 mm.[1] posterior to it, is circular, measures 0·1 mm. in diameter and carries a low broad papilla in the depths of the very small atrium into which it leads. I could not find a suctorial muscle around it other than the continuation of the general body muscles. Otto and Duff state that there is a suctorial muscle, but my examination of Duff's material strengthens me in the belief that there is no such muscle. Fischoeder, moreover, states that there is none. The centre of the acetabular orifice is 3·0 mm. posterior to the genital pore and 1·8 mm.[1] from the posterior extremity. Its orifice is large (0·70 mm. in diameter), circular, and tilted obliquely ventrally.

The triangular form, due to dorsal ridging, originally ascribed to the worm by Rudolphi, could doubtfully be made out microscopically in the specimens at hand and not at all grossly. The histological cross sections vary in form at different levels, but are never fairly subtriangular. Anteriorly they are subcircular, with an inconstant gentle dorsal depression at the right of the mid-line. This shortly disappears, the intercaecal portion of the dorsum becoming flat, and at the level of the genital pore strongly concave. Below this point the venter in turn becomes markedly flattened and now a gentle median dorsal swelling appears, to disappear at the anterior border of the acetabulum. Between the genital pore and the latter level the transverse diameter of the worm is to the dorso-ventral as 3 : 2. The venter between the acetabular orifice and the anterior acetabular margin is now strongly concave (obliquity of plane of section due to tilting of acetabulum). At the level of the acetabular orifice the venter resumes its convexity (and maintains it to the terminus) the section here appearing subcircular with flat or concave dorsum. Below this level a distinct median dorsal swelling appears, which continues a short distance (0·2 mm.), disappears for a distance of 0·064 mm. to re-appear for a second (0·2 mm.) course. After this one of the declivities gradually disappears, the other forming

[1] Measurements taken from the entire specimen 5·95 mm. long.

one side of a cleft which indents the worm fairly deeply. The cleft gradually becomes shallower, finally disappearing toward the posterior extremity.

From the above description it will be seen that the dorsal ridge of Rudolphi (1814) is represented in the specimen here studied by a short, low, rounded median discontinuous ridge extending 0·4 mm. over the dorsum of the worm, i e. only about one-sixth of its length. To the writer it seems to be a very inconspicuous character on which to name the species.

The surface is smooth and glistening except near the genital pore, where the cuticle is thrown into deep transverse ridges. There are no spines, tubercles or ridges anywhere.

The acetabulum is large, subterminal, tilted obliquely ventrally, and measures 1·45 mm. laterally, 1·0 mm. dorso-ventrally and 0·92 mm. antero-posteriorly.

The cuticle agrees in general structure with that of other trematodes; it shows no spines or other specializations. Duff discusses the subcuticular cells and their function with considerable detail; she considers the "large cells" in the suctorial muscles as embryonic remnants rather than nervous elements.

The Alimentary System.

The oral orifice leads into a roomy oral cavity of subglobular shape measuring 0·6 mm. in width, 0·22 mm. dorso-ventrally and 0·384 mm. antero-posteriorly. From its postero-lateral portion, two blind tubular evaginations, one on each side and each 0·2 mm. long, extend into, but not through, the muscle of the oral sucker. Fischoeder takes issue with Otto here. The former found the oral cavity very small, of triangular shape in cross section with one angle directed ventrally and the two pockets springing from the other two angles. The latter describes the cavity as a cleft (Spaltförmig). It seems possible that the variation might depend upon different degrees of rigor mortis in the oral suctorial muscle or to the kind of preservative used. The oral cavity is surrounded by a muscle 0·25 mm. thick in the form of a much flattened sphere measuring 1·1 mm. dorso-ventrally, 1·1 mm. in width and 0·9 mm. antero-posteriorly. At its most anterior portion its fibres are arranged into two closely placed sphincters, the more anterior being the heavier. They do not lie *at* the oral orifice, but well (fully 0·25 mm.) internal thereto. The beginning of the oral cavity thus assumes a broad, short, tubular form lined by cuticle and not surrounded by special muscle.

The oesophagus passes from the centre of the posterior portion of the oral cavity, is very short, simple, *and surrounded by a heavy muscular coat*, a continuation of the muscle of the oral sucker, together with large and numerous so-called salivary cells. In addition, a notable sphincter is present at the oesophago-oral junction; this muscle has been commonly missed by other writers. The oesophageal muscle continues over the bifurcation to include both arms of the caeca, accompanied laterally by cuticle and subcuticular cells, but no "salivary" ones. Here again there has been no agreement among writers. Otto is very positive about an oesophageal muscle being present while Duff and Fischoeder are silent about it. The caeca are broad, not branched, lightly sinuous and pass at once to the lateral borders which they follow posteriorly, each caecum ending blindly behind the acetabulum close to cuticle. The caeca contain black granular material and vegetable cells, they are notably constricted in places, forming sacculations above and below, one so large as to closely approach the size of the oral sucker. Upon reaching the acetabulum the caeca pierce the vitellaria which lie close to the cuticle, shortly emerging close to the cuticle with vitelline follicles still present mesially but not laterally.

THE REPRODUCTIVE SYSTEM.

The male organs. The testes are preequatorial, precacetabular, lie ventral to and between the caeca and antero-posteriorly to each other, the anterior but slightly to the right and but slightly ventral to the posterior. The posterior border of the hind testis lies slightly posterior to the equator, reaches almost to the acetabulum and one or two of its branches extend slightly below the level of the anterior acetabular border. The anterior border of the anterior testis extends well forward beyond the ventral border of the oral sucker. Each consists of an irregular, small body from which six to eight long, wavy, coarse, tube-like branches extend. They are mostly bifid and extend in all directions; a few occur ventrally, whilst by far the greatest number extend dorsally between the caeca. The branches thus come to overlap the neighbouring testis, while their fields[1] overlap and almost coincide. On account of their branching character their whole mass is difficult to estimate, but it is about equal to that of the oral sucker and certainly much less than that of the acetabulum. Spermatozoa were numerous in the body and branches of the testes in both worms that were sectioned.

[1] Nomenclature advocated by Stiles.

In the second yet more immature specimen (the one sectioned longitudinally and which had been compressed) the testes appear differently. They are elongated dorso-ventrally and well separated from each other, the dorsal halves of each are quite smooth, branches projecting radially from the ventral portions only. The branches are short and comparatively straight, and the anterior testis lies distinctly ventral to the posterior one.

The right vas efferens originates in the anterior testis (which is therefore the right testis), emerging from the right side of the base of a heavy dorsal branch. It curves posteriorly for a very short distance (0·112 mm.), and, at the level of the genital pore arches anteriorly and laterally, gaining the mesial wall of the right caecum; hugging this closely, it passes anteriorly and slightly dorsally but always intercaecally. The left vas efferens emerges from the body of the inferior testis, posteriorly and slightly to the left of the mid-line and approximately mid-way between its anterior and posterior borders. It passes anteriorly and slightly dorsally being surrounded at first by testicular branches, but soon it attains and follows the caecum like its fellow. The two caeca converge rather quickly post-bifurcally and unite well dorsally immediately anterior to the most anterior testicular branch. The vas deferens is short, and not provided with musculature; it quickly bends ventrally and posteriorly (accompanied at this point by the uterus) forming a moderately (at one point only notably) dilated and closely coiled vesicula seminalis externa. The latter pierces a pyriform cirrus pouch lying slightly to the left of the median line, anterior to the genital pore, and immediately anterior to the posterior border of the oral sucker. Its long axis extends obliquely from a left, anterior and dorsal point toward the right, posteriorly and ventrally, its broader extremity directed dorsally; it measures 0·3 mm. in length, 0·18 mm. wide, and its walls are moderately thick, 0·02 mm. They taper finely at the end which encloses the cirrus. The vesicula seminalis interna makes one or two close turns, becomes very narrow and continuous with the short poorly developed cirrus[1]. The interval between the coils and the cirrus wall is occupied by a fine reticulum holding numerous (prostatic?) cells. The tip of the penis occupies a chamber which passes into a very fine ejaculatory duct, that unites *in* the genital papilla with the metraterm. Spermatozoa were not found anywhere in the tubular portions of this system.

Variations from the foregoing were noted as follows in the more

[1] Otto does not note the cirrus.

immature specimen which was sectioned longitudinally. First, the wall of the cirrus pouch thinned so rapidly toward the narrower extremity that it was quite lacking before the cirrus was reached. Second, the chamber holding the cirrus was contracted to very small dimensions, and quickly narrowed to a fine tube.

Duff (p. 89), describes the testes as lobed, and so figures them in Fig. 1. In Fig. 4, however, she shows sections of *branches*, and my study of her microscopic preparations shows that they are really branched, as in my own material.

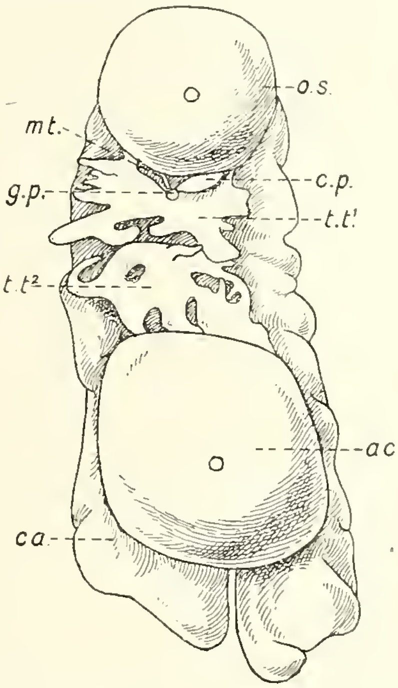

Fig. 1. Drawing from photograph of wax reconstruction of internal anatomy. Ventral view: *o.s.* oral sucker; *m.t.* metraterm; *g.p.* genital papilla; *c.p* cirrus pouch; *t.t.*[1] anterior testis: *t.t.*[2] posterior testis; *ac.* acetabulum; *ca.* caeca.

The female organs. The ovary is median or sub-median, dorsal, and contiguous to the anterior portion of the acetabulum. Its zone does not extend anterior to the acetabular zone. It is subspherical, appears subtriangular posteriorly in cross section and subquadrilateral anteriorly; it measures 0·224 × 0·25 mm. and 0·35 mm. dorso-ventrally. The oviduct passes from its dorsal aspect approximately mesially and extends a short distance dorsally and posteriorly, where it effects a junction with Laurer's canal, dorsal and close to the shell gland in the median line. It then makes three or four easy turns in this region and

at once pierces the shell gland, becoming continuous with the much broader oötype. The shell gland is median, posterior to the ovary, and contiguous to the acetabulum; it measures 0·184 × 0·21 mm. and 0·220 mm. dorso-ventrally; it is irregular in shape, deeply indented sinistro-ventrally by the oötype and is suddenly attenuated posteriorly and anteriorly, the latter process extending well to the right and slightly overlapping the ovary. The oötype lies embedded between the shell gland dorsally and the acetabulum ventrally, slightly to the left of the median line; within it there is a finely granular and reticular blue material (sections stained by haematoxylin and eosin) female germ cells, vitelline granules and spermatozoa; it measures 0·07 mm. broad, 0·14 mm. long and has very thin walls. Laurer's canal begins at about the mid-point of the oviduct as above described, it follows the latter closely anteriorly, extending directly to the ovary where it suddenly bends dorsally, makes one or two easy spirals and ends dorso-median at the level of the origin of the oviduct and 0·448 mm. anterior to the excretory pore. It does not cross the excretory vesicle or duct and is not provided with a receptaculum seminis.

The uterus passes from the left side of the oötype, in contact with the dorsum of the acetabulum and slightly left of the median line; it coils intricately in this region, passing anteriorly and dorsally to the ovary, showing its closest turns in this region; it now passes anteriorly with a few easy turns in the dorsum of the worm, dipping ventrally once between the testicular branches and the caeca on either side. Just above the level of the cirrus pouch it turns sharply ventrally and arches over the anterior testis; here it runs closely parallel to the vas deferens, lying to the left of the same; it passes now slightly posteriorly and ventrally to the right side of the cirrus pouch, uniting with the ejaculatory duct to form the hermaphroditic canal. This is very fine and lies in a broad, low genital papilla situated in a single genital atrium. The genital pore shows no trace of a sphincter, much less a sucker.

At numerous positions, and in practically all parts of its course, the uterus dilates into aneurysm-like structures three to eight times the diameter of the rest of the tube. Here the cuboidal epithelium is replaced by a flat squamous type and the lumen contains a blue granular material, sometimes a few pink (vitelline) granules or vitelline cells and occasionally a primitive germ cell. Nowhere are fully developed ova found, from which it follows that the specimen described was immature. This absence of ova, or at most the presence of but a solitary undeveloped one, is opposed to the view of Otto who believed that the

thinner portions of the uterus were due to the internal pressure of the ova. It would appear from the findings here that the sacs are developmental features, and of hereditary rather than acquired nature. Additional weight is lent to this view by the occurrence of one or two places of thinning which are not distended. Spermatozoa were not found in this tube except close to the oötype.

The vitellaria consist of two roughly triangular structures occupying the posterior two-thirds of the worm; the broader side of each triangle is convex and follows the body margin; the other two sides are concave, and their angle of junction is directed toward the ovary. The vitellaria consist of very small sparse follicles containing minute quantities of pink granules; as already stated above, each mass is pierced by the caecum. The courses of the ducts are not surely made out either in their transverse or longitudinal portions. In the specimen here studied a vitelline reservoir is easily made out close to the shell gland and to the right of the same, but a communication with the genital tube on the one hand, or with the vitellaria on the other, could not be established. Other writers disagree upon the arrangement of the terminal vitelline apparatus; Otto states that two transverse ducts form a common longitudinal one which enlarges posteriorly to reservoir proportions, that it then narrows markedly and unites with the genital tube shortly posterior to the point where it is joined by Laurer's canal; Fischoeder describes the vitellaria as emptying into a paired, distinct reservoir, but does not state the manner of its communication with the genital tube. The extent of the vitellaria farther forwards is a little different in this specimen from what has been described by other authors. Otto limits the vitellaria to the posterior third, and other writers to the posterior half. The vitellaria were especially sparse in the specimen cut longitudinally. The obscurity of these ducts is probably explained by the immaturity of the specimens.

The ova teased from the uterus of the largest specimen are oval, not operculated, and measure 0·13—0·15 × 0·085—0·09 mm.

THE MUSCULAR SYSTEM.

Apart from the features which have already been noted, the suckers do not vary from the plan usually found in other Amphistomidae. The subcuticular musculature varies in one respect. i.e. the bundles occurring over the venter are much more robust than those of the margin and dorsum. The increase in their size here is so marked as to seem scarcely

due to contraction (in production of body flexion), such as I have seen in *Fasciola hepaticum* and *Fasciolopsis buski.*

The Excretory System.

Fine channels lead to the posterior end of the specimen, where there is a small excretory vesicle. The latter begins below toward the tip of the caeca, 0·288 mm. from the body extremity, as two long, tubular, bilateral spaces lying closer to the cuticle than to the acetabulum. They unite at the level of the excretory pore and continue anteriorly as one vesicle, which, in the specimen studied, was of irregular shape, and apposed to the acetabulum. Here it attains its greatest size, at most but little larger in bulk than the ovary, and gradually narrows anteriorly to disappear at the level of the oötype. Its duct takes origin from the dorsum of the vesicle at its broadest part, anterior to its bifurcation, and passes posteriorly dorsal to the vesicle, ending dorso-median at the level of the acetabular orifice and 2·2 mm. from the posterior extremity. The anterior portion of the vesicle is lined by a very tall columnar "epithelium," apparently the most highly specialized "epithelial" cell in the worm; this lining is continued posteriorly over the dorsum of the vesicle until the internal ductal orifice is reached, into which it passes for a short distance. Coarse pink hyaline droplets appear to exude from it into the vesicle. Duff states that it is surrounded by thick spongy muscular walls.

The Nervous System.

The course of nerve fibres and the localization of the ganglia could not be determined in my material, but other authors agree in describing a ring of perioesophageal ganglia from which three nerve trunks extend on each side anteriorly and one on each side posteriorly with commissural fibres between the posterior trunks. Finer fibres are distributed from the commissures and trunks to the reproductive and excretory organs.

Systematic Position.

The full diagnosis of the systematic units concerned are available in the works of Fischoeder and of Stiles and Goldberger, for which reason their names only will be given here, as follows: Superfamily PARAMPHISTOMOIDEA; Family Paramphistomidae; Subfamily Cladorchinae; Genus *Cladorchis*; Subgenus *Stichorchis*. Its important special features are, in brief, the presence of: a cirrus pouch, two pharyngeal diverticula, a two-ringed pharyngeal sphincter and branched

(klados, a branch) testes lying one above (stichos) the other. With the exception of the new superfamily, the above classification follows that given by Fischoeder. Reference to Stiles and Goldberger's work will show that this new high unit is a justifiable one (p. 15) but that my material will not fit in with their lower rank diagnosis (pp. 169 and 170) of *Cladorchis* and *Stichorchis* largely on account of the question of musculature of the genital atrium. Dr Stiles informs me that he would be inclined to separate this beaver fluke from both *Cladorchis* and *Stichorchis* and make it the type of a new genus on the basis of this lack of a genital sucker. This would certainly be necessary to

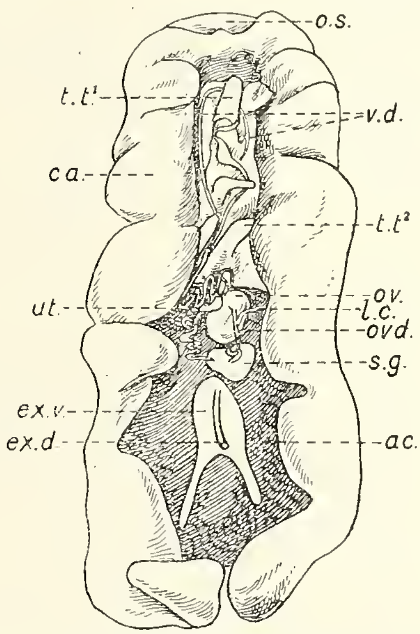

Fig. 2. Drawing from photograph of wax reconstruction of internal anatomy. Dorsal view: *o.s.* oral sucker; *v.d.* vas deferens; *t.t.*[1] anterior testis; *t.t.*[2] posterior testis; *ca.* caeca; *ov.* ovary; *ut.* uterus; *ovd.* oviduct; *s.g.* shell gland; *ex.v.* excretory vesicle; *ex.d.* excretory duct; *ac.* acetabulum; *l.c.* Laurer's canal.

accommodate it to Stiles and Goldberger's classification. I feel personally that the several lots of material should be collected and reviewed before reaching a final conclusion, paying special attention to (1) whether the genital atrium is or is not musculated, (2) the oesophagus musculated or not (Otto says it is musculated in the Amphistomidae in general), (3) presence of cirrus, (4) general anatomy of vitelline system, (5) oesophageal sphincter.

This paper contributes perhaps more to the subject of the development than to that of the anatomy of this fluke. In respect to the

anatomy emphasis is laid on certain individual features which have not been generally recognized although they have been pointed out by some writers. These features are: the pre-oesophageal sphincter, oesophageal musculature and heavy ventral subcuticular musculature. From the point of view of development the minor branching of the testes has been noted by other authors and it has been assumed that the testes become more complex with maturity. Previous writers make no reference to vitelline development. That this development occurs at a late stage is best shown by reference to my second specimen (Fig. 2) wherein but a few follicles are noted; the late development may explain why the ducts could not be traced in my material.

The absence of any inflammatory changes near the fluke, and the good nutritional condition of the host indicate that the worm is a commensal parasite, this impression being strengthened by observance of vegetable fibres in its caeca.

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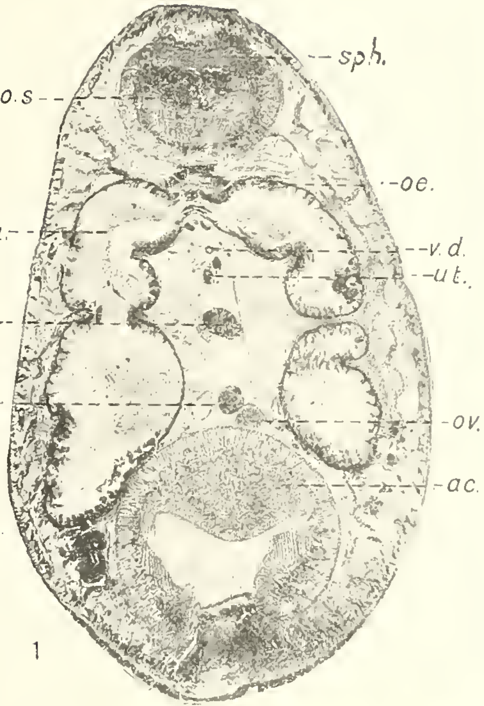
DESCRIPTION OF PLATE V.

Fig. 1. Longitudinal section through immature, artificially flattened specimen (no. 2). *sph.* oral sphincter; *o.s.* oral sucker; *oe.* oesophagus; *ca.* caeca; *ov.* ovary; *a.t.* anterior testis; *p.t.* posterior testis; *v.d.* vas deferens; *ut.* uterus; *ac.* acetabulum. The testes are sectioned through their dorsal halves. Note their lack of branching in this immature specimen.

Fig. 2. Transverse section at junction of second and third body fifths through posterior testis. *t.bod.* body of testis; *t.br.* testicular branches; *ca.* caeca; *ut.* uterus; *vit.* vitelline follicles. Compare robustness of ventral and dorsal cuticular muscles.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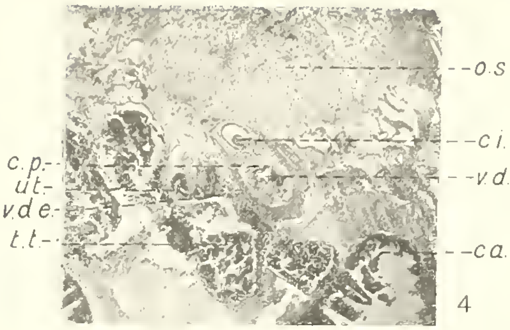
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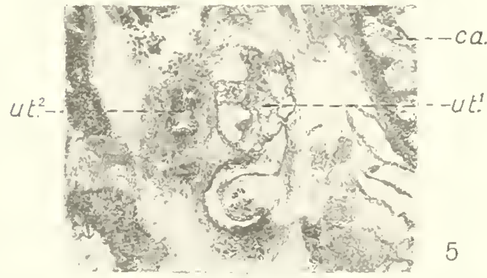
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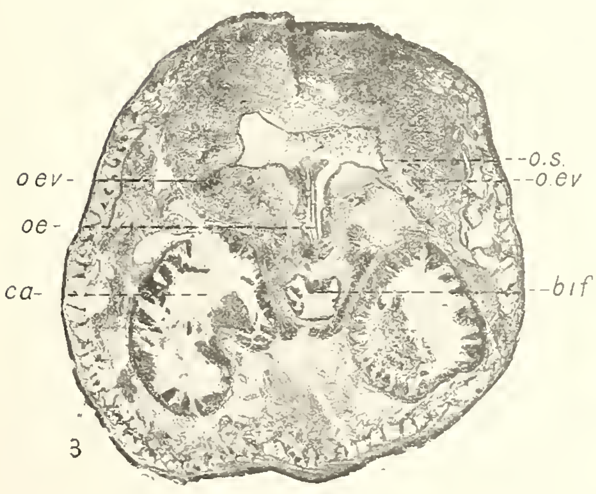
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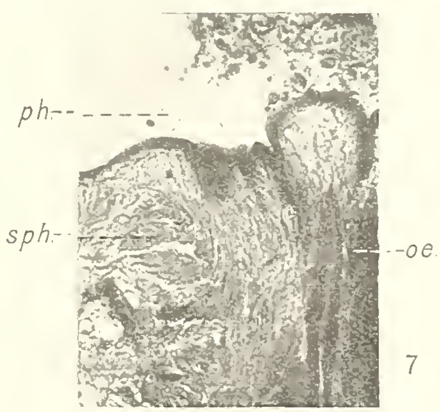
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Fig. 3. Transverse section to show oral evaginations and muscular character of oesophagus. *o.ev.* oral evagination; *o.s.* oral sucker; *oe.* oesophagus; *ca.* caeca; *bif.* bifurcation of oesophagus.

Fig. 4. Transverse section immediately posterior to oral sucker. *o.s.* oral sucker; *c.p.* cirrus pouch; *ci.* cirrus; *t.t.* testicular branches; *v.d.i.* vas deferens interna; *ut.* uterus; *v.d.e.* vas deferens externa; *ca.* caeca.

Fig. 5. Transverse section cut close to Fig. 2, more highly magnified. Note absence of ova in uterine dilatations. The reticular material therein stains faintly blue with haematoxylin and eosin. *ca.* caeca; *ut.*[1] dilatation of uterus; *ut.*[2] non-dilated part.

Fig. 6. Transverse section through portion of ventral body wall, *cut.* cuticle; *c.m.* circular muscle; *d.m.* diagonal muscle; *l.m.* longitudinal muscle.

Fig. 7. Transverse section through oesophagus cut close to Fig. 3 and more highly magnified, *sph.* oesophageal sphincter; *oe.* oesophagus; *ph.* pharynx.

A NOTE ON THE PERIOD DURING WHICH THE EGGS OF *STEGOMYIA FASCIATA* (*AËDES CALOPUS*) FROM SIERRA LEONE STOCK RETAIN THEIR VITALITY IN A HUMID TEMPERATURE[1].

By A. BACOT, F.E.S.

(*Entomologist to the Lister Institute.*)

It is well known that the eggs of the above-named mosquito remain viable when out of water for many months. Various workers, among whom may be named Theobald, Newstead, Francis and Mitchell, record varying periods up to nine months' duration.

Howard, Dyar and Knab (1912) state that with some species of *Aëdes* the eggs may remain dormant over a year. It does not seem to be so generally recognised, however, that the eggs *when immersed in water* may remain dormant. Marchoux, Salimbeni and Simond (1903), and Dupree, according to Mitchell (1907), were acquainted with the fact. The French investigators record a period of 70 days and Mitchell one of over a year. I think, Goeldi, as quoted by Howard, Dyar and Knab (1912), must have encountered the phenomenon but he considered the dormant eggs to be dead, at least it is in this light that I view his statement that submerged eggs perish. Bacot (1916) showed that immersed eggs may remain dormant for five months. It is apparently essential to the retention of vitality under conditions of drought and dormancy, when submerged, that the eggs shall have been incubated, development within the egg having proceeded up to the stage of the larva being ready for immediate hatching.

[1] Since this Note went to press a batch of some 2000 or 3000 eggs of this mosquito, laid during April 1916, was tested after 15 months' storage. The eggs had been laid on filter paper and were placed in a wax card jar kept in the cool room (ca. 9° C.) of the Lister Institute. All the eggs were placed in a pan of tap water; a few hatched within 24 hours, and others responded later to the stimulus of the addition of a little *B. coli* culture to the water. Twenty adults were reared.

So much by way of preface seems needful in explanation of the following detached notes.

On my return from Freetown in August, 1915, I brought home a batch of ova of *Stegomyia fasciata*, and from these eggs reared adult mosquitoes. During November, 1915, a large supply of eggs was obtained with the object of ascertaining the extreme period of viability of eggs stored out of water but in a humid atmosphere.

The eggs, laid on filter paper, were placed in a waxed card jar with a waxed paper cover and kept in an unused ice chest in a cool cellar. This cellar has a bricked but uncemented floor and shows a very even range of conditions; the temperature seldom showing more than one or two degrees' variation between night and day, while the percentage of humidity is always high. Although circumstances did not permit of constant readings during 1915 and 1916, a fairly complete daily record exists for the period between November, 1910, and February, 1912. Monthly averages based on this, together with a chart showing curves of maximum and minimum temperatures and the humidity are published in the Plague Supplement III of the *Journal of Hygiene*, 14th January, 1914, pp. 456 and 461. From this it will be seen that the fluctuations of temperature within a period of 16 months lie between 6·6° C. (44° F.) to 17·8° C. (64° F.) while the record of humidity is even more stable, the monthly averages only varying between 91 and 95 %.

Some thousands of eggs were stored and the numbers used in the experiments were correspondingly large. Time did not permit of detailed counting, but the round figures given may be taken as approximately correct, being the outcome of estimates, backed by considerable experience of actual counts.

The immersion tests of the eggs were commenced 7 months after laying.

Tested after	Result
7 months.	Eggs hatched readily during July, 1916, probably not more than 10–20 % of the larvae failing to emerge.
9 ,,	Eggs hatched readily on 31 August, 1916.
10 ,,	On 2 October, 1916, a very noticeable rise in the percentage of failures to hatch was observed. Some of the larvae, however, quitted their eggs within two hours of immersion.
11 ,,	On 4 November, 1916, only a few of the eggs immersed yielded larvae; probably not more than 5 %, yet some of these quitted the shells within an hour of immersion. Four adults were reared within 10 days and 8 more within 12 days.
12 ,,	On 4 December, 1916, 5 larvae emerged from about 600 eggs, but none earlier than 5 or 6 hours after immersion. All the larvae were full-

grown within 7 days, and two male specimens were reared within 10 days, the other three took longer, but the most backward larvae had pupated by the 9th day.

Over 13 months. On 12 January, 1917, a single larva emerged from a batch of about 1000 eggs. It hatched within 24 hours of immersion and pupated within 7 days; a male specimen was reared within 10 days.

On 15 January, 1917, some 14 to 15 months after laying, the remainder of the eggs (upwards of 1000) were immersed, but all failed to hatch.

It is of course possible that the temperature conditions were unfavourably low during the storage of the eggs for a race of the insect occurring in West Africa. Although none of the eggs stored out of water by Bacot (1916) in Freetown retained their vitality for more than 8–9 months, it might be objected that this was owing to the humidity factor being unfavourable and that in a saturated atmosphere a higher temperature than that of the cellar used in this experiment would allow of an extension of the period of viability. As against this, the facts concerning the period of viability when immersed must be considered. The longest period of dormancy noted in regard to submerged eggs under natural conditions (in West Africa) was 5 months, and although in an incubator at 24° C. (75° F.), in London, I have had several equally long records of dormancy, and one of 7 months, the conditions were admittedly unnatural in that the eggs had been externally sterilized and then placed in sterile fluids.

Mitchell's record (1917, p. 26) relating to the survival of the eggs when immersed in water for over a year, is unfortunately unaccompanied by any details that suggest close observation. In another passage (p. 148) this author places the limit at 9 months, while the looseness of phraseology as indicated by the statement "as the single eggs will resist drying almost indefinitely" leaves one in doubt as to whether the periods mentioned are the result of exact observation or conclusions based on general experience.

I venture to call the attention of American investigators to the desirability of further evidence on this point. Though I am prepared to find that the period may be longer than my evidence shows, it seems to me possible that the African and American races of *S. fasciata*—to suggest no smaller division—may differ considerably in constitution. Personally I am inclined to consider that the cool conditions did not affect the viability of the eggs experimented with and that so far as eggs of West African origin are concerned, the extreme period of viability of eggs stored out of water may be taken to be about a year.

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NOTES ON TICKS.

BEING DESCRIPTIONS OF TWO NEW SPECIES OF *ORNITHODORUS* AND OF THE HITHERTO UNKNOWN FEMALE OF *HYALOMMA MONSTROSUM*.

By CECIL WARBURTON, M.A., F.Z.S.

(*From the Quick Laboratory, University of Cambridge.*)

(With 3 Text-figures.)

Hyalomma monstrosum, Nuttall and Warburton, 1907 (*Proc. Camb. Phil. Soc.*, Vol. XIV. pp. 392–416, figs. 41–45 of the ♂). The female is here described for the first time.

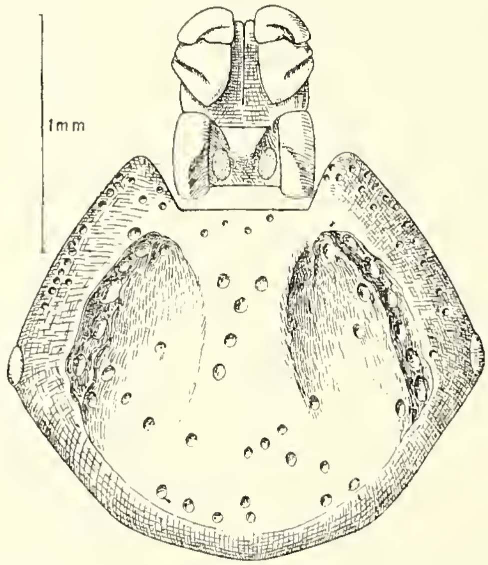

Fig. 1. *Hyalomma monstrosum* ♀. Capitulum and scutum.

Female: *Scutum* rather broader than long (1·7 × 2 mm.), very dark, glossy, with a few large, deep, conspicuous punctations; cervical grooves deep at their origin, their floors rugose; lateral grooves a series of

deep, more or less confluent punctations; the lateral ridges continued as a narrow dark border round the posterior end of the scutum; a few smaller punctations on the scapulae and on the antero-lateral borders; about 20 large, deep punctations in the median area. Emargination deep; eyes small and inconspicuous; scapular angles rounded.

Capitulum: Basis rectangular, distinctly divided into three regions —two broad glossy lateral ridges and a median depressed area containing the porose areas; these are long-oval and parallel, the interval rather greater than their breadth; cornua short and massive. Palps like those of the ♂ but with art. 3 less salient laterally. Dentition 3 | 3.

Ventral surface: Spiracle of the same character as that of the ♂, but somewhat broader. Legs like those of the ♂.

Described from a specimen taken from *Sus cristatus* near Barhi, Hazaribagh District, by Major O. A. Smith, in company with *H. bispinosa* var. *intermedia*, and *R. haemaphysaloides*. (Indian Mus., no $\frac{2172}{17}$.)

The ♂ was described (N. and W. XII. 1907) from a specimen taken from a horse in the Chin Hills, E. of Chittagong, and sent to us by Mr Maxwell Lefroy. We have since seen three ♂'s—two taken from a buffalo, Agul, Bengal, 31. VII. 1909, by Mr J. L. Bose, and sent to us by Mr Howlett, and one taken in the Bombay Presidency in 1912, host unrecorded, now in the Indian Museum (no. S.P.A. 383). One of Mr Bose's specimens we were allowed to retain and it is in our collection (N. 1220). These males conform precisely to the original description except that the "festoon-like bags" behind the anal plates are sometimes less conspicuous. It is with some hesitation that we assign this tick to the genus *Hyalomma*.

Ornithodorus piriformis n. sp.

Adults small, about 3·5 mm. long, notably piriform in shape, especially when not fully distended; brown, with legs and palps often yellow. Integument rough, with very numerous close-set mamillae, among which the discs are fairly conspicuous. Hairs on integument and dorsal surface of the legs very short and rather thick, but not clavate. Camerostome without movable "cheeks." Anus midway between the genital aperture and the posterior border; a well-marked transverse fold (or paired organ) placed very posteriorly (as in *O. megnini*). Two additional lateral folds or slits level with the anus.

Capitulum rather small, well overlapped by the bluntly-pointed hood; hypostome small and feebly armed, bearing very small teeth

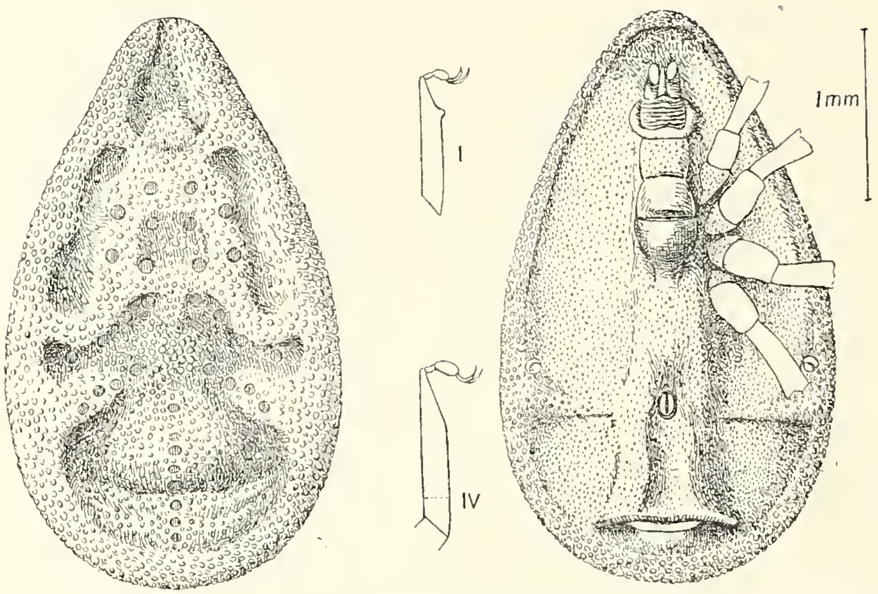

Fig. 2. *Ornithodorus piriformis* ♀, dorsal and ventral aspects, tarsi I and IV.

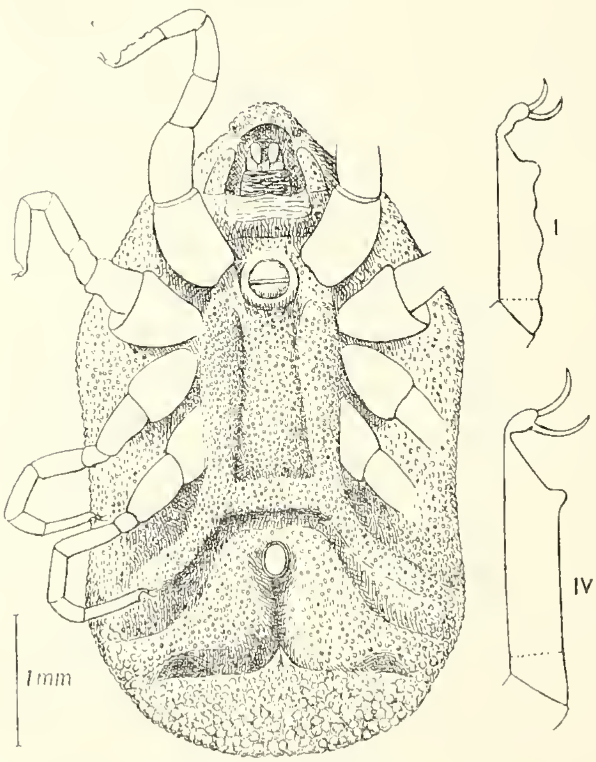

Fig. 3. *Ornithodorus asperus* ♂. Ventral aspect, tarsi I and IV.

(2 | 2) on its lateral borders. Bristles on the basis capituli inconspicuous, but two are present at the origin of the hypostome, near the middle.

Legs. Coxae small, subequal, slightly chitinised, differing little in texture from the general ventral surface; all the tarsi long and sharp-pointed; tarsus I prominent in the region of Haller's organ, but otherwise without humps; tarsi II–IV tapering gradually to a point. Pads distinctly large for Argasidae.

Described from 15 specimens taken at Mahabaleshwar, Satara District, at a height of 4200 ft. (? host) by F. H. G., 13–16. iv. 12. Indian Mus. $\frac{\text{S.P.A}}{10}$.

The only known *Ornithodorus* with similar tarsi is *O. talaje*, but from this it is easily distinguished by the absence of movable "cheeks" to the camerostome, as well as by its much finer mammillation.

Ornithodorus asperus n. sp.

Resembling *O. talaje* in size, shape and general configuration, and possessing, like *O. talaje*, movable "cheeks" to the camerostome, and similar ventral folds and posterior paired organ.

Easily distinguished from *O. talaje* by its integument and its tarsi. The integument is very finely mammillate, the mammillae being much smaller and more pointed than in *O. talaje*, giving the whole surface a very rough texture. Simple hairs, short, but longer than in *O. talaje*, are scattered over the surface. They are longer and rather conspicuous on the hood. The tarsi are distinctly humped, and the dorsal surface of tarsus I is raised in a succession of slight rounded elevations (see Fig. 3) (the tarsi of *O. talaje* taper without any prominences).

Hypostome well furnished with sharp teeth at its distal extremity. Four bristles under the basis capituli.

Described from a single specimen, numbered 296 in the Berlin Museum, and taken on the Bileck Steppe, Mesopotamia by Dr Kohl, of the Expedition of Baron M. v. Oppenheim, 22. v. 1913. No host recorded.

ON THE OCCURRENCE OF HYDATID CYSTS IN MONKEYS.

By WILLIAM NICOLL, M.A., D.Sc., M.D., D.P.H. (London).

(*From the Lister Institute of Preventive Medicine.*)

In 1909, Professor McIntosh of St Andrews University sent me a cyst from the abdominal cavity of a South African baboon, *Cynocephalus porcarius* Budd. The cyst, which was single, had been ruptured in removal, part of its contents had escaped, and some blood had entered it. The cyst measured about 20 mm. in diameter, was a typical hydatid, and resembled in its general structure the ordinary simple unilocular hydatid of man.

Attached to the cyst wall and scattered throughout the grumous contents were numerous scolices. These were ovo-globular in outline and measured on an average 0·215 × 0·175 mm. The head or body of the scolex measured 0·095 × 0·12 mm. while the tail measured 0·12 × 0·055 mm. The four suckers measured approximately 0·054 mm. in diameter but the size varied from 0·042 mm. to 0·063 mm.

The head was surmounted by a double row of hooks, rather straight in type, and measuring 0·021–0·027 mm. in length. The average number of hooks was 38.

As is well known the hydatid tapeworm which passes its adult stage in carnivores, particularly dogs, is one of the most widely distributed parasitic worms known. It occurs in greatest profusion in countries and districts where dogs or other *Canidae* are numerous and especially where there are many cattle and sheep. Few parasites, however, possess such an extensive and varied list of intermediate hosts and the number of species of animals known to function as such probably exceeds forty.

Man, unfortunately, is by no means an uncommon intermediate host and is only too frequently fatally affected. Short of death the parasite gives rise to many symptoms of the most serious nature, the only remedy for which in most cases is operative treatment.

Amongst the numerous animals which figure as intermediate hosts mention may be made of cattle, sheep, pigs, deer of various kinds, goats, horses, donkeys, dogs, rabbits, kangaroos, etc. Several species of monkeys and apes are also already known as hosts of hydatids, for instance, *Inuus cynomolgus*, *Inuus ecaudatus*, and *Theropithecus silenus*. The camel, dromedary, giraffe and tapir also figure amongst the intermediate hosts. It would in fact appear as if all the larger Mammalia are possible hosts. It would indeed be of considerable interest to discover any species of the larger mammals which can be shown conclusively to be immune to infection with this parasite.

DOLICHOPERA MACALPINI N. SP., A TREMATODE PARASITE OF AUSTRALIAN POISONOUS SNAKES.

By WILLIAM NICOLL, M.A., D.Sc., M.D., D.P.H. (London).

In 1911, I received from Dr Georgina Sweet of Melbourne University, two lots of Trematodes stated to have been collected respectively from the intestine of the tiger snake, *Notechis scutatus*, and the lungs of the copperhead snake, *Denisonia superba.* In 1916, Dr Burton Cleland, of the Bureau of Microbiology, Sydney, sent me two tubes containing similar parasites, obtained from the peritoneum of an unidentified snake killed on Flinders Island.

In sending me her material Dr Sweet informed me that an unnamed parasitic Trematode had been described from the copperhead snake by McAlpine[1] in 1891, and a comparison of the specimens with his description led me to the conclusion that they were identical with those observed by that writer.

McAlpine's description, so far as it goes, is clear and easy of interpretation. His promise of a more detailed account has to the best of my knowledge not been fulfilled, and the present paper is an attempt to remedy this omission.

In investigating some Queensland Trematodes I encountered in the intestinal canal of a carpet snake, *Python variegatus,* two specimens of a Trematode which bore a close resemblance to those from the above-mentioned snakes. The resemblance, however, was only a general one and there was no hesitation in separating the forms as distinct species. The forms from the carpet snake were designated the type of a new genus, *Dolichopera,* and the form observed by McAlpine was provisionally included in the same genus under the name *D. macalpini*[1].

The normal habitat of McAlpine's species is somewhat doubtful. He himself commented upon this, as he found the parasites not only

[1] It should be remarked that McAlpine's specimens were inadvertently referred to the tiger snake but at the same time the scientific name quoted was that of the copperhead snake.

in the lungs and trachea but also in the mouth, gullet, and stomach. He remarked that it is most unusual to find the same species of fluke inhabiting both the respiratory and alimentary systems, an opinion which I can only endorse, except in the few cases in which the same parasite inhabits both the trachea and the oesophagus. The matter, however, is further complicated by Dr Sweet's observation of the parasite in the intestine of the tiger snake, unless, as is not impossible, the stomach was regarded as part of the intestine. The most probable explanation of Dr Cleland's finding the parasites in the peritoneum appears to be that the lungs were damaged on killing the snake or in dissecting it and that the parasites thereby made their escape into the peritoneal cavity.

In my original description of *Dolichopera parvula*, from the carpet snake, the habitat was recorded as the intestine, but this should in reality have been the oesophagus. It is possible that a similar *lapsus* may account for Dr Sweet's observation in the case of the tiger snake. Taking everything into consideration therefore it seems most probable that the normal habitat of these two species is the lungs, trachea and oesophagus. As already noted a similar habitat is met with in the case of certain other Trematode parasites of reptiles.

McAlpine describes the colour of the parasites as "quite black." This, however, only applies to the older specimens in which the dense mass of the uterus fills almost the entire body, leaving only a narrow clear rim round the margins. In less mature specimens, and particularly in those from the tiger snake, the general colour is dark brown.

The parasite is moderately flat, elongated oval in outline, with rounded ends. The posterior end is frequently drawn out into a short tip-like projection. In addition there is not uncommonly a slight constriction just behind the ventral sucker. The surface of the body is covered with fine spines which extend to within a short distance of the tip of the tail.

The length varies from 2·6 mm. to 3·5 mm. (average 3·1 mm.). The maximum breadth, which occurs at the level of the ventral sucker, is 1·0–1·6 mm. (average 1·25 mm.). The length is therefore about $2\frac{1}{2}$ times the breadth.

The subterminal oral sucker is fairly conspicuous and measures 0·315–0·465 mm. in diameter. The ventral sucker lies almost exactly in the centre of the body, or a very short distance behind it. Its outline is generally somewhat obscured by the uterus. It is smaller than the oral sucker, measuring only 0·25–0·45 mm. in diameter.

The pharynx is contiguous with the oral sucker and measures 0·15 × 0·135 mm. The oesophagus is extremely short and divides almost immediately into the diverticula. These pass down along the sides of the body but their course is greatly obscured by the uterus. Their terminations however are conspicuous, lying between the testes and the yolk glands in the posterior third of the body. They curve round the posterior borders of the testes and their ends are usually turned in towards the middle line, and do not quite reach the tip of the tail.

The genital aperture lies to one side of the oral sucker, on the level of its posterior border. Usually it is on the right side but not infrequently on the left. The cirrus pouch is a comparatively enormous structure stretching from the genital aperture obliquely backwards to near the middle of the ventral sucker. Its course is somewhat sinuous and its breadth fairly uniform. It contains a large vesicula seminalis, a short pars prostatica and a moderately long ductus ejaculatorius.

The testes are situated in the posterior third of the body, separated from the tip of the tail by a space almost equal to their length. They lie alongside each other but somewhat oblique, the left being in advance of the right. They are elongated oval in shape and of large size, measuring 0·23 × 0·135 mm. They are overlapped by the uterus only to a very small extent, along their anterior border.

The ovary lies on the right side about midway between the ventral sucker and the testes, and entirely obscured by the uterus. It is a small globular body measuring about 0·075 mm. The yolk glands are entirely lateral and confined to the outer side of the intestinal diverticula. They extend from the anterior border of the ventral sucker to the ends of the intestinal diverticula. The follicles are of moderate size.

The uterus, as already mentioned, is extremely voluminous. It consists of a narrow highly convoluted tube. In younger specimens it is thrown into the form of a semicircular festoon surrounding the ventral sucker except on its anterior border. The convolutions obscure the ovary and intestinal diverticula and overlap the testes to a variable extent. In the most mature specimens the uterus increases enormously in extent and the individual convolutions become largely obliterated. Additional convolutions are thrown down over the testes and in many specimens the latter are almost entirely covered. The anterior part of the body also becomes filled with the uterus right up to the oral sucker with the result that the cirrus pouch is completely obscured. The mass of eggs extends up to the genital aperture. In such specimens

the only organs which remain visible are the oral sucker, the yolk glands and the ends of the intestinal diverticula. The numerous eggs are brownish-yellow to dark brown and measure 0·028–0·032 × 0·018–0·019 mm.

It is evident that this species, though bearing a considerable resemblance to *Dolichopera parvula*, differs from it in several important respects. In the first place *D. parvula* is a much smaller form. The ventral sucker is situated further back. The testes and yolk glands are relatively further from the tip of the tail, while the yolk glands are much less extensive. The cirrus pouch is very much shorter and smaller, and the uterus is situated for the greater part in front of the ventral sucker. In some respects these differences appear to be of much more than specific value but from various considerations it appears inadvisable at the present moment to separate these two forms generically.

REFERENCE.

McAlpine, D. (1891). Remarks on a Fluke Parasite in the Copper-head Snake. *Proc. Roy. Soc. Vict.*, n.s., iii. 40–43.

ARE *ENTAMOEBA HISTOLYTICA* AND *ENTAMOEBA RANARUM* THE SAME SPECIES? AN EXPERIMENTAL INQUIRY[1].

By CLIFFORD DOBELL.

Imperial College of Science.

(*Report to the Medical Research Committee.*)

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Introduction.

Nobody who studies the parasitic amoeba of the frog (*Entamoeba ranarum*) and the dysentery amoeba of man (*E. histolytica*) can fail to be struck by the remarkable resemblance between these organisms. The development of the former I described for the first time in 1908 and 1909, since when I have had exceptional opportunities of studying the latter; and I can state, with some confidence, that there is no constant structural character which will permit of a distinction being drawn between these two species. The active amoebae can usually be readily distinguished from one another by the inclusions (food bodies) in their protoplasm, but not by their own nuclear and cytoplasmic structure; but the precystic amoebae, devoid of all food bodies, and the cysts, at every stage in their development, are so closely alike that preparations of the one could be used as demonstration specimens of the other.

[1] The experiments here recorded were carried out, in the spring and early summer of 1916, at the Imperial College of Science with the aid of a grant from the Medical Research Committee. Publication has been delayed through pressure of other work.

This truly remarkable resemblance has not excited the notice which it merits. No doubt this is largely due to the fact that, at the time when I described the life-history of *E. ranarum*, that of *E. histolytica* was imperfectly known and incorrectly described. The development of the cysts of *E. histolytica* (then supposed to belong to two other different species, "*E. tetragena*" and "*E. minuta*") was wrongly interpreted by all observers until 1911, when E. L. Walker first showed that it conforms to that which I described in *E. ranarum*. That this is so is now generally recognized, and from my own observations I have no doubts about the matter: indeed, I pointed out in 1909 that the development of the cysts of *E. histolytica* was probably "almost identical" with that of *E. ranarum*. But it has taken so long for the comparatively simple and true story of the development of *E. histolytica* to obtain recognition, in place of the fictitious and complicated accounts of the earlier German workers, that the observations which I made some ten years ago appear to have been forgotten. I recall these facts not only to vindicate my original account of *E. ranarum*, which has several times been called in question (but which was, nevertheless, the first correct description of the development of the cysts of any intestinal amoeba of the group to which the dysentery amoeba of man belongs), but also to direct attention to the close similarity of *E. ranarum* to *E. histolytica*—a similarity which suggested the experiments described in the present paper.

When the very close resemblance of these two species is realized, the question naturally arises whether there may not really be something more than a mere similarity—in fact, an actual identity of the two species, *E. histolytica* and *E. ranarum*. Is it not possible that the harmless amoeba of the frog becomes, when accidentally introduced into the intestine of man, the pathogenic agent of human amoebic dysentery? I have myself been accustomed to raise this question in my lectures for some years past, and in conversation and correspondence with those engaged in studying amoebic dysentery: and recently Alexeieff (1914) has made the same suggestion in print. The question can clearly be answered only by experiment. It is possible to attempt to infect human beings with *E. histolytica* by means of the cysts of *E. ranarum*: and conversely, to infect frogs with *E. ranarum*, by feeding them upon the cysts of *E. histolytica*. The former is obviously the more direct method of experiment, but not easily practicable. The latter is less direct, but is easy of trial, and is that recorded in the following pages.

THE EXPERIMENTS.

At first sight it might appear a simple matter to endeavour to infect frogs by feeding them upon material containing cysts of *E. histolytica.* It is, however, not so simple, as will be evident from the following considerations, which determined the method of experimentation which I adopted.

If *E. histolytica* and *E. ranarum* are two forms of the same parasite, then the cysts of *E. histolytica*, when ingested by a frog, would develop into *E. ranarum* in this host; and an experimentally infected frog would, if subsequently examined, be found to harbour amoebae indistinguishable from those which might occur in it in nature. It is therefore necessary to be quite certain, before attempting to infect frogs by means of *E. histolytica* cysts from man, that the frogs themselves are not already infected with *E. ranarum.* Now this is a matter of great difficulty. We can discover that a man is infected with *E. histolytica* by examining his faeces and finding the cysts of the amoeba in them. But with *E. ranarum* and the frog the matter is very different. I have never succeeded in ascertaining with certainty, by examining its faeces for cysts, whether an adult frog is, or is not, infected with *E. ranarum* at most seasons of the year. A frog which is heavily infected—as can be ascertained by killing it and examining the contents of its large intestine—does not pass cysts as a rule in its faeces. Without killing the frog, therefore, it is usually impossible to discover whether it is, or is not, infected.

In the course of observations extending over several years, I found stages in the encystation of the amoeba, and fully formed cysts, in the contents of the large intestine only during winter (when the frog normally neither feeds nor passes faeces) and early spring; that is to say, in the months immediately preceding the breeding season of *Rana temporaria* and *R. esculenta* in England and Germany. I have also found cysts of *E. ranarum* in the faeces passed by infected frogs during the breeding season, but at no other time. This fact led me to believe that the life-history of *E. ranarum* has—like that of *Opalina* and other parasites of the frog—a definite relation to the seasonal activities of its host. It appears to me most probable that *E. ranarum* lives and multiplies in the gut-contents of the frog during the greater part of the year, but does not encyst: but during the winter and early spring, when the frog ceases to feed and defaecate, the amoebae encyst, and are thus ready to escape and to infect fresh individuals when passed into the water by the

host at its breeding time. It might therefore be supposed that the frog generally gets infected with *E. ranarum* while still a tadpole—the faeces of the adults infecting the young, just as in the case of *Opalina*. In support of this supposition, the fact may be adduced that tadpoles in nature are sometimes found to harbour *E. ranarum* in their intestines. This has been confirmed by Collin (1913).

Taking all these facts into consideration I therefore decided to attempt to infect tadpoles with *E. ranarum* by feeding them upon material containing cysts of *E. histolytica*: since it seemed to me probable that it is the tadpole—not the adult frog—that normally acquires the infection in nature, and since it is possible to obtain tadpoles which are known with certainty to be uninfected with *E. ranarum* before they are used for experiment.

The experimental tadpoles were obtained by artificially fertilizing the eggs of the frog (*Rana temporaria*) in the laboratory. In order to ensure that no contamination of the tadpoles should occur from cysts of *E. ranarum* in or on their parents, the cultures were made in the following way[1]. The eggs and spermatozoa were removed from the frogs after they had been pithed. The skin was previously sponged with alcohol, and care was taken to avoid injury to the intestine in removing the genital products. The eggs were then placed in large glass dishes, fertilized, and covered with carefully filtered tap-water[2]. All instruments and dishes used were previously sterilized with boiling water. As an additional control, in case any of the tadpoles should subsequently prove to be infected with protozoa or other organisms, I made a careful examination of the gut-contents of every frog used in the experiments. None of them contained any stages of *E. ranarum*, though the usual other parasites were present in abundance (*Opalina, Nyctotherus, Balantidium, Eimeria, Trichomonas, Trichomastix, Octomitus*, and the trematode *Opisthioglyphe rastellus*). As none of these parasites was subsequently found in the tadpoles in any culture, it may be concluded that the precautions taken were adequate.

In this manner four cultures of tadpoles were obtained from four different crosses. In the first two (which I may call *A* and *B*), a large number of eggs hatched, producing a plentiful supply of tadpoles: but in the other two, only a small percentage of the eggs developed, and

[1] I am greatly indebted to Mr H. G. Newth, Demonstrator in Zoology at the Imperial College, for his assistance in making the cultures at a period when my time was very fully occupied with other work.

[2] As noted below, one culture was made with unfiltered water.

the few tadpoles obtained were therefore mixed together into a single culture (C). After hatching, the tadpoles were allowed to remain undisturbed for a few days, during which time they fed upon the remains of the jelly from the eggs. The remains of this were then removed, the dirty water replaced by clean filtered water, and the cultures then subdivided for the experiments.

Culture A was divided into three parts—subcultures A_2 and A_3, with the remains of the original culture kept as a control (A_1). Culture B was similarly divided into five subcultures, B_2, B_3, B_4, B_5, and the original as control (B_1). Culture C, containing very few tadpoles, was divided into two—subculture C_2, and control (C_1). I thus had seven subcultures for feeding experiments, and three control cultures containing tadpoles derived from the same parents and bred in exactly the same way.

The attempts to infect the tadpoles by feeding them upon cysts of *E. histolytica* were all made in the same way, and may therefore all be described together. A quantity of human faeces—varying in amount in different cases—which contained large numbers of cysts of *E. histolytica*, was placed in a glass tube. This was then put into the dish containing the tadpoles to be experimented upon, and allowed to remain. I had but little doubt that the tadpoles would eat the faeces, and at the same time the cysts, without any further inducement; for in nature they eat the excrement of other animals, and decaying organic matter of all sorts. My expectations were more than realized. The tadpoles greedily devoured the human faeces as soon as it was offered to them. Indeed, they seemed greatly to prefer it to any other food with which I attempted to feed them; and the tadpoles so reared, in spite of the filthy condition of the water in which they lived, were very healthy. They grew rapidly, and in two cultures attained a larger size than those in the controls. Not only did they eat the original human faeces with avidity, but they continued to ingest and reingest it many times after it had passed through their bodies. I several times observed a gorged tadpole still gorging itself upon human faeces, whilst another simultaneously devoured the long coil of faeces protruding from its anus. There was never any doubt, therefore, that the tadpoles would have abundant opportunities of infecting themselves, if this were possible, with any cysts or organisms present in the original human faeces.

The seven different experimentally fed subcultures were fed upon faeces from seven different convalescent carriers of *Entamoeba histolytica*. In every case I examined the faeces carefully before giving it to the

tadpoles, in order to ensure that it contained a large number of mature (quadrinucleate) and healthy cysts.

The tadpoles were allowed to continue feeding upon the infected faeces as long as they would do so. At the end of two or three weeks, little or none of the original faeces was usually discoverable, and the bottoms of the culture dishes were covered with fine débris and numerous coils of tadpole faeces which seemed no longer attractive to them—probably because the material had lost its nutritive value with repeated passage through their bodies. From this stage onwards I fed the tadpoles on finely minced meat, or human faeces from persons who, as I determined by frequent examination of their stools, were free from infection with *E. histolytica*. The water in the cultures was renewed from time to time, when necessary, the old and dirty water being siphoned off and fresh filtered tap-water substituted.

As already noted, the tadpoles fed on human faeces remained very healthy and throve exceedingly. Those which were not killed for examination finally underwent partial—a few of them complete—metamorphosis before the cultures were finally abandoned. I examined the intestinal contents of a few tadpoles every day, or every few days, after they had begun to feed on the infective material. I did this in the following way. A tadpole which had fed on faeces (easily determined, because the faeces in the intestine is clearly visible through the transparent belly-wall of the living tadpole) was removed from the dish, killed by decapitation, and its gut removed entire with needles and placed upon a slide. The gut was then slit open from end to end, and the contents mixed and spread out in a few drops of Ringer's fluid. The preparation was then covered with a coverglass and examined under the microscope. At first I examined the entire contents of the intestine, but with increase in size this became impossible. I therefore examined in this way a few samples of the gut-contents taken from different parts of the intestine. When the large intestine had become differentiated I usually confined my examination to this part only, as it is the seat of infection with *E. ranarum* in the adult frog. From time to time I also examined the coils of faeces dropped on the bottoms of the culture dishes by the tadpoles; and also the remains of the infected human faeces, so long as there were any, to see whether living cysts were still present. All the findings were carefully recorded from day to day.

All the experiments led to practically the same result. It is therefore unnecessary to give the individual records for each culture. The tadpoles in some cultures were examined more frequently than those in

others, but apart from this the results of the examination of subcultures A_2, A_3, B_2, B_3, B_4, and C_2 were closely similar. As culture B_3 was followed for the longest period, I will give the results of the examinations made upon these tadpoles as an illustration of the findings in general. (The differences observed in other cultures will then be briefly indicated.)

Subculture B_3.

Eggs fertilized March 16, 1916.

Tadpoles fed on human faeces containing immense number of ripe *E. histolytica* cysts, March 24.

Tadpoles killed and examined on following dates:

March 26. Gut-contents of tadpoles contain a very large number of apparently quite healthy and unchanged *E. histolytica* cysts. No amoebae or other free organisms.

March	27.	The same; but some dead cysts also found.
,,	28.	Same as preceding.
,,	29.	The same, but dead cysts rather more plentiful.
April	2.	Many cysts still present, but the majority dead.
,,	5.	Fewer cysts, mostly dead.
,,	16.	A very few cysts found with difficulty; all appear dead.
,,	21.	No cysts or free organisms discoverable in gut-contents.
,,	27.	Same as April 21.
May	3.	,, ,,
,,	11.	,, ,,
,,	12.	,, ,,
,,	13.	,, ,,

It will be evident from the foregoing that living cysts, but no amoebae, were found in the tadpoles fed on infected human faeces until the 12th day after the first feed. During this time the proportion of dead cysts gradually increased. On the 23rd day only a very few dead cysts were found; and thereafter, until the 50th day, none.

The other five subcultures mentioned above gave similar results, only differing in the dates at which cysts (all dead) were last found in the gut-contents. These dates were as follows:

A_2	Cysts	last	seen on	23rd	day
A_3	,,	,,	,,	20th	,,
B_2	,,	,,	,,	6th	,,
B_4	,,	,,	,,	19th	,,
C_2	,,	,,	,,	9th	,,

It should be noted with regard to subculture B_2 that no tadpoles were examined between the 6th and the 28th days after feeding. This was because the cysts, both in the tadpoles and in the human faeces, were found to be so scanty and difficult to find on the 6th day, that a more intensive study of this culture seemed likely to be unprofitable. Similarly in C_2; when the tadpoles were examined on the 8th day, they were found to contain nothing but dead cysts, though these were plentiful; and the culture was therefore not examined again until the 24th day, when all trace of cysts had disappeared.

It is evident that the cysts of *E. histolytica*, even when ingested repeatedly, undergo no further development in the gut of the tadpole. They will continue to pass through the gut until they die, which may take as long as three weeks. They do not, when ingested, establish an amoebic infection in the tadpole, as they might be expected to do if they were identical with those of *E. ranarum*. All the tadpoles remained consistently uninfected with *Entamoebae* from the time when they first fed upon the cysts until they were completely metamorphosed.

It appears to me probable, indeed, that the cysts of *E. histolytica* were entirely unaffected by their passage through tadpoles, and would have survived for the same time if they had merely been placed in water. I made some experiments to determine this point, with the following results:—In nearly every case the cysts of *E. histolytica*, when kept in a large volume of water, survived for times closely similar to those observed for the cysts passing through the tadpoles. Many cysts were generally alive at the end of a week, some at the end of two weeks, but most were dead at the end of three weeks. Occasionally living and apparently quite healthy cysts were discoverable after three weeks; and in a single experiment I found a few seemingly perfectly intact cysts, which had lain in water for five weeks after leaving the human body. Drying immediately kills the cysts of both *E. histolytica* and *E. ranarum*; and in faeces undiluted with water it is seldom that living cysts can be found after the lapse of about two weeks[1].

In my experiments I judged the cysts to be dead when they showed disintegration and vacuolation of the protoplasmic contents, both in the fresh condition and after fixation and staining. At times also I used the "eosin test[2]," but not as a rule. Its results were consistent and confirmatory, but its employment seemed to me unnecessary.

[1] These findings agree on the whole with earlier records; cf. Dobell (1909), Kuenen and Swellengrebel (1913), Wenyon and O'Connor (1917).

[2] Cf. Kuenen and Swellengrebel (1913), Wenyon and O'Connor (1916).

In the foregoing experiments I examined altogether 160 tadpoles at various times after they had fed upon human faeces containing cysts belonging to seven different strains of *E. histolytica.* The number is not enormous, but is, I think, quite sufficient to demonstrate that the cysts will not undergo development in the tadpole. The time and trouble necessary for the examination of even a single tadpole are considerable. Long before I had examined the last I had convinced myself that the experiments were a complete failure, so far as infection was concerned. I wished, however, to establish beyond question the fact that infection is impossible, and I regret that my time was too fully occupied to allow me to examine more tadpoles. The experiments, though not absolutely conclusive from a statistical point of view, have convinced me at all events that a tadpole, however abundantly fed with cysts of *E. histolytica,* will not, in all probability, acquire as a result an infection with *E. ranarum.*

Since none of the experimental tadpoles became infected with *Entamoebae* the examination of those in the control cultures became almost a work of supererogation. For the sake of completeness, however, I examined at various times 40 tadpoles from the control cultures A_1, B_1, and C_1. They were all completely negative for free or encysted *Entamoebae* or any other protozoa, as was to be expected. It should be added that the controls were fed upon cooked meat or vegetables, and one of them (B_1) also with human faeces free from cysts of *E. histolytica.* They all remained active and healthy to the last, and displayed no features of special interest.

No detailed mention has so far been made of subculture B_5. This was a very small culture containing only eight tadpoles, which were taken from the control culture B_1 about a month after the eggs had hatched. As I had at this time satisfied myself that the tadpoles in the other cultures were not becoming infected with *Entamoebae,* it occurred to me that the temperature at which the experiments were made might possibly influence the result. All the cultures had previously been kept at the ordinary temperature of the laboratory, and I therefore determined to make some similar experiments with cultures kept at higher temperatures. Unfortunately it was very difficult with the means at my disposal to maintain a large culture at a constant high temperature; and in addition the tadpoles, when the temperature of the water was raised considerably, appeared extremely uncomfortable and refused to feed. With subculture B_5, however, I succeeded in keeping them for three days at a temperature of 32·5° C., during which time they fed upon human faeces containing abundant living *E. histolytica* cysts

given in the usual way. On the third day I examined a tadpole, and was somewhat surprised to find that although it contained a great many cysts they were all dead and much disintegrated, many consisting of merely a cyst wall containing a few granules. On examining the remains of the human faeces left in the water in the culture dish, I found that in this also the cysts were in the same condition. I then put the culture at the ordinary laboratory temperature once more. Two tadpoles died shortly afterwards, and only a few dead cysts were found in them. The remaining five tadpoles were killed and examined on the 14th day after feeding. In three of these I could find no cysts; but in the other two I found, after much searching, a very few bodies which I believed to be the remains of cysts. They were so far disintegrated that their identification was rather doubtful.

At the higher temperature, therefore, as at the lower, the attempt to infect tadpoles with *E. histolytica* failed completely. The cysts did not develop in any way; they merely degenerated in the tadpoles and in the water with greater rapidity than before, so that after three days at the higher temperature they had reached a stage in degeneration comparable with that seen after three weeks at the lower. It seems probable, therefore, that *E. histolytica* cysts will survive much longer in cold than in warm water.

A further point in connexion with one of the cultures (A_2) is worth recording. This culture was made with unfiltered tap-water—not with filtered water like the others. It was a very large culture, containing several hundreds of tadpoles. On examining a tadpole from it on the 16th day after they had been fed on human faeces—at a time when most of the *E. histolytica* cysts were dead—I found some small but active amoebae creeping about in the gut-contents. On closer examination these proved to be typical free-living amoebae of the *Amoeba limax* type, with characteristic nuclei, contractile vacuoles, etc. Many other tadpoles in this culture were subsequently found to be infected also. Examination of the faeces of the tadpoles on the bottom of the dish showed that the amoebae were here present in vast numbers. It seemed clear, therefore, that the *limax* amoebae had, in some way, gained access to the culture; and the tadpoles had evidently swallowed them with the faeces on which they were living. It is somewhat remarkable, however, that the amoebae had established themselves in the intestines of the living tadpoles. I had no difficulty in satisfying myself that this was really the case, by taking suitable precautions to avoid contamination of the gut-contents in removing it for examination.

On examining the droppings of these tadpoles from the bottom of the dish, I found other free-living protozoa in them. These were several ciliates (*Pleuronema, Plagiopyla*, etc.), and flagellates (a species of *Bodo*, etc.) which were all forms that I have at different times obtained from London tap-water. They were therefore probably introduced into the culture with the unfiltered water employed in making it. I was in doubt, however, whether the *limax* amoeba had been introduced in the same way, or whether it might have come from the human faeces on which the tadpoles had been fed. Fortunately I was able to determine this point. I happened to have kept a small quantity of this original faeces in a corked glass tube; and on examining it, I found that the same *limax* amoeba had developed in it in large numbers. It therefore appears highly probable that the faeces upon which the tadpoles were originally fed contained the cysts of the amoeba, which hatched in the water and so contaminated the culture. It may be added that the mortality was much higher in this culture than in any of the others; but whether this was in any way connected with the infection of many of the tadpoles with the *limax* amoebae I have no means of judging.

So far as I am aware experimental "parasitization" of any animal with free-living amoebae has not previously been achieved, though the occurrence of similar forms in the gut-contents of several animals has been recorded. I have myself described[1] a natural infection of the lizard with an amoeba apparently related to *A. limax*.

In the course of the experiments with cysts of *E. histolytica* I had an opportunity of observing also the behaviour of the cysts of some other human intestinal protozoa in their passage through the tadpole. The human faeces containing *E. histolytica* cysts, employed in the experiments, contained also, in some instances, the cysts of *Entamoeba coli, Giardia* (= *Lamblia*) *intestinalis*, and *Chilomastix* ("*Tetramitus*") *mesnili*. All of these behaved precisely alike. They passed unchanged through the gut of the tadpole, until they finally degenerated and died. The time taken in this process was closely similar to that which I observed for cysts left standing in clean water. Passage through the gut of a tadpole appeared, therefore, to have no effect upon any of the cysts.

These results were such as might have been foretold, for the most part: for an amoeba like *E. coli* is not found in the frog, and the frog's lamblia (*Giardia agilis*) is conspicuously different[2] from that of man

[1] Dobell (1914). It may be added that the so-called "*limax* amoebae" described in the *fresh* faeces of human beings were probably in most cases the parasitic *Entamoeba nana*. Cf. Dobell and Jepps (1917).

[2] Cf. Alexeieff (1914).

(*G. intestinalis*). With *Chilomastix*, however, the case is different, for the species found in frogs (*Ch. caulleryi*) is so like that of man (*Ch. mesnili*) that Alexeieff (1914) has even suggested that they are the same. As this is a possibility not to be ignored, I devoted some further attention to it, beyond the incidental observations made during the experiments with *E. histolytica* cysts. On July 17, 1916, I fed some of the surviving tadpoles in culture B_2—which I had previously failed to infect with *E. histolytica*—on human faeces containing an immense number of healthy cysts of *Chilomastix mesnili*. I examined some tadpoles on the 21st, 22nd, 27th and 28th of July, and found, as before, that the cysts passed through them quite intact. By July 28th (11 days after first feeding) the cysts were nearly all dead, but none of them appeared to have undergone any development. They were still present in fairly large numbers in the intestines of the tadpoles and in their droppings on the bottom of the culture dish.

I conclude from these observations that the cysts of *Ch. mesnili* will not develop in the tadpole; and consequently that *Ch. mesnili* Wenyon and *Ch. caulleryi* Alexeieff—parasitic in man and frog respectively—are probably, in spite of their close resemblance, quite distinct species. I have not myself studied the cysts of the parasite of frogs, though the flagellates have been known to me since 1907; but according to the brief account of them by Alexeieff (1912) they appear to be almost identical with those with which I am very familiar in the faeces of man[1].

Discussion of Results.

The experiments just recorded afford no support for the hypothesis that *Entamoeba histolytica* and *E. ranarum* are merely two forms of the same species inhabiting two different hosts. It is now certain, since the experimental work of Walker and Sellards (1913), that man becomes infected with *E. histolytica* by swallowing the cysts of the parasite; and it is highly probable, though not yet experimentally proved, that the frog similarly acquires an infection with *E. ranarum* by swallowing the cysts of this species. But it seems legitimate to conclude, from the experiments here described, that the cysts of *E. histolytica* pass, when ingested, unchanged through the intestine of the frog. They do not undergo any development in this host, and thereby establish in it an entamoebic infection. It seems highly probable, therefore, that the cysts of *E. histolytica* and those of *E. ranarum*, in spite of their very close resemblance, are in some way different from one another. This

[1] Cf. Dobell and Jepps (1917).

difference may be expressed by saying that *E. histolytica* and *E. ranarum* are, in all probability, different species. This is the chief conclusion which I draw from the foregoing experiments.

I do not, of course, ignore the fact that biological classification rests fundamentally upon morphology—upon structural and not upon functional characters. When, therefore, I draw the above conclusion from physiological data only—from an observed difference in the behaviour of the cysts of the two different "species"—I do not imply that such data are, alone, sufficient to establish a specific difference. I take them as an indication that *E. histolytica* and *E. ranarum* differ from one another in important functional characters; and that the difference is so considerable, that when the life-histories of both species are fully known, it will then be found that they are likewise distinguishable morphologically. There is already direct evidence that this is so: for the early development of *E. ranarum* in the tadpole, as described by Collin (1913), appears to be quite different from anything known to occur in the life-history of *E. histolytica* in man. It is, however, still premature to discuss these points, since the life-history neither of *E. histolytica* nor of *E. ranarum* is yet known in complete detail.

Nor is it justifiable to conclude directly, from the fact that *E. histolytica* cysts will not give rise to an *E. ranarum* infection in the frog, that a converse infection is equally impossible. It is still possible that the cysts of *E. ranarum*, if swallowed by a man, might infect him with *E. histolytica*, and thus make him suffer from amoebic dysentery. It is still possible, though perhaps improbable, that *E. histolytica* and *E. ranarum* are the same species: but that after the amoeba has established itself in man, its cysts have ceased to be infective for the frog. In any case, the transference from the cold-blooded to the warm-blooded host would have to be accompanied by extensive changes in the habits of the parasite. It would have to change from a harmless commensal, feeding upon the contents of the intestine, into a pathogenic parasite living upon its tissues. At present there is no indication that such a change is possible.

It must be confessed that the hypothesis that *E. histolytica* is the human form of *E. ranarum*—a natural parasite of amphibia, accidentally acquired by man—is not without attractiveness. It would agree very well with the distribution of amoebic dysentery and its seasonal incidence. If true, it would also suggest certain preventive measures directed against the frog. There is, however, as yet no direct evidence to incriminate the frog as a source of amoebic infection in man, and in tropical

countries at least it seems unnecessary to look beyond the native population for the "reservoir" of amoebic dysentery. It is not, of course, excluded that *E. histolytica,* though now a distinct species proper to man, may possibly have been acquired by him originally from a closely similar parasite of amphibia. This, however, is a mere guess which can never be tested, and is based solely on the striking similarity of *E. histolytica* and *E. ranarum* at the present day.

Taking all the foregoing points into consideration it seems, therefore, justifiable to draw the following conclusion: *Entamoeba histolytica* Schaudinn and *Entamoeba ranarum* Grassi are probably distinct species; and consequently the frog, in all probability, is not a "reservoir" of human amoebic dysentery.

NOTE ON THE SPECIFIC NAME OF THE *ENTAMOEBA* OF HUMAN AMOEBIC DYSENTERY.

In the foregoing pages I have called the *Entamoeba* which causes amoebic dysentery in man *E. histolytica.* As, however, a number of workers[1], notably in France, have recently reintroduced the name *E. dysenteriae* for this organism—professedly in deference to the Rules of Nomenclature—I wish to state briefly my reasons for not adopting this name.

Everybody competent to judge now agrees that there is but a single species[2] of *Entamoeba* which has been proved to cause dysentery in man. This is the species which was called *Entamoeba histolytica* by Schaudinn (1903), *E. tetragena* by Viereck (1907), *E. africana* by Hartmann (1907), *E. minuta* by Elmassian (1909), and probably by several other names by other workers. All the specific names proposed since 1903, when the name *histolytica* was introduced, are, of course, no longer valid, now that the identity of the organisms concerned is recognized. There is no difficulty, therefore, in deciding the claims to priority of the names just cited.

The real difficulty regarding the nomenclature of the intestinal amoebae of man was introduced by Schaudinn in his attempt to clear up the confusion which existed when he wrote. Up to that date (1903) there was great confusion, not only in the nomenclature, but also concerning the facts. It was generally supposed that there was but a single species of amoeba—the "*Amoeba coli*" of Lösch—parasitic in the human bowel. By some it was considered pathogenic, by

[1] Cf. Brumpt (1913), Alexeieff (1914), Mathis and Mercier (1916), etc.

[2] Of this species there are, however, several different varieties or strains, distinguishable morphologically by the size of their cysts. Cf. Wenyon and O'Connor (1917), Dobell and Jepps (1917).

others harmless. It is to Schaudinn's credit that he recognized that there were really two different species confounded with one another—one harmless, the other pathogenic. As both had received the same name at different times, he therefore proposed to restrict the specific name *coli* to the one, while introducing a new specific name (*histolytica*) for the other, and simultaneously referring both to the genus *Entamoeba*. In principle Schaudinn acted strictly in accordance with the Rules of Nomenclature. But most unfortunately he assigned the name *E. coli* to the harmless amoeba, and introduced the new name *E. histolytica* for the pathogenic form. If he had studied the question more carefully, he would have discovered that Lösch's "*Amoeba coli*" was the very form for which he proposed the name *E. histolytica*. It is impossible, I believe, for anybody to read Lösch's very careful account of his amoebae, supported as it is by his *post-mortem* findings and illustrations, and reach any other conclusion[1]. Whatever confusion may have been introduced by subsequent writers, there is no evidence at all that Lösch studied more than one species, or that he confused two together: and there is no real doubt as to which that species was. It was the species which causes dysentery, and which Schaudinn renamed *E. histolytica*. The correct name of this organism is, therefore, according to the Rules of Nomenclature, *Entamoeba coli* Lösch; and the name *E. histolytica* is a synonym without validity.

It is to be noted that Schaudinn was completely unjustified in his revision of the name "*Amoeba coli*." Not only should he have retained the name *coli* for the pathogenic species, but he should also have refrained from introducing any new specific names at all. The harmless amoeba, which he wrongly called "*E. coli*," had already not only been observed and recognizably described by Casagrandi and Barbagallo (1895), but also named by them (in 1897) *Entamoeba hominis*. Accordingly, this is probably the "correct" name of the organism now generally known as "*E. coli*."

Now although the name *E. coli* can claim priority over all others as that of the dysentery amoeba, the name *E. dysenteriae* clearly has no such claim. This name ("*Amoeba dysenteriae*") was proposed by Councilman and Lafleur in 1891 for *the very same organism as that to which Lösch gave the name "Amoeba coli*[2]." They proposed to change

[1] This appears to be the opinion also of Brumpt (1913), Wenyon (1915), Mathis and Mercier (1916), and others.

[2] "We have called the organism, which was first described by Lösch under the name of amoeba coli, the 'amoeba dysenteriae.' The name given to it by Lösch is not distinctive." (Councilman and Lafleur, 1891, p. 405.)

its name merely because they regarded it as *inappropriate*. There is no justification, in the Rules, for such a procedure: and there is therefore no doubt that *dysenteriae* Councilman and Lafleur is a synonym for *coli* Lösch, and must therefore give place to the latter if the Rules are to be followed. In other words, the argument which seeks to displace *histolytica* in favour of *dysenteriae*, will, if pursued further, likewise displace the latter in favour of *coli*.

Most unfortunately, everybody has agreed to give the name *E. coli*, in conformity with Schaudinn's proposal, to the large harmless amoeba inhabiting the human colon: and since 1903 an extensive literature has grown up in which this name is almost universally used with this signification. It will thus lead to nothing but the most unnecessary confusion if we propose to adhere strictly to the letter of the law in this case, and transfer to the pathogenic species the name which, by universal consent, the non-pathogenic species has borne for fourteen years. In my opinion it would defeat the very object for which the International Rules were framed—the avoidance of confusion and the maintenance of order in zoological nomenclature—to transfer the name *E. coli* from the large harmless amoeba of the human colon to the dysentery amoeba. For my own part, I prefer to accept Schaudinn's mistake in its entirety, and to continue to call the harmless amoeba *E. coli*, the dysentery amoeba *E. histolytica*. This is, at least, a consistent course to follow. For whether we call the dysentery amoeba *histolytica* or *dysenteriae*, we defy the law of priority. The "correct" name of the organism is *coli*—a name which can be used with complete justification by all who, regardless of the confusion which they will bring, insist upon the letter of the law. It is, however, somewhat inconsistent to replace the name *histolytica* by *dysenteriae* because the latter has priority, since it is only in defiance of the rule of priority that the name *dysenteriae* can itself be used.

In such a case as this, it seems to me that it would be better to modify the Rules themselves rather than to transpose and change names which are almost universally received; and it is to be hoped that an agreement in this matter, acceptable to all, may be reached before long[1]. Continual changing—or still worse, transference—of zoological names is a constant

[1] It is to be hoped that this matter may be decided when another International Zoological Congress can be held. I may remind the reader that it was decided at the last meeting (Monaco, 1913), that exceptions to the law of priority could be admitted, by general consent,

(i) When a name to be transposed had been in general use for 50 years previous to 1890,

(ii) When an older and "correct" name had not been used in scientific literature for 20 years.

It will be noted that these grounds for exception do not apply to the case here considered.

source of annoyance to zoologists. When it affects both zoology and medicine, however, it is like to become intolerable.

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